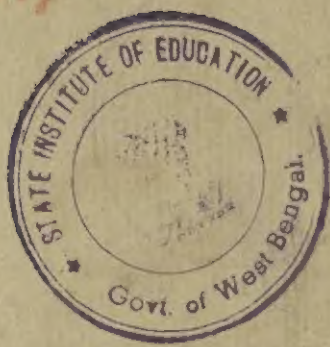
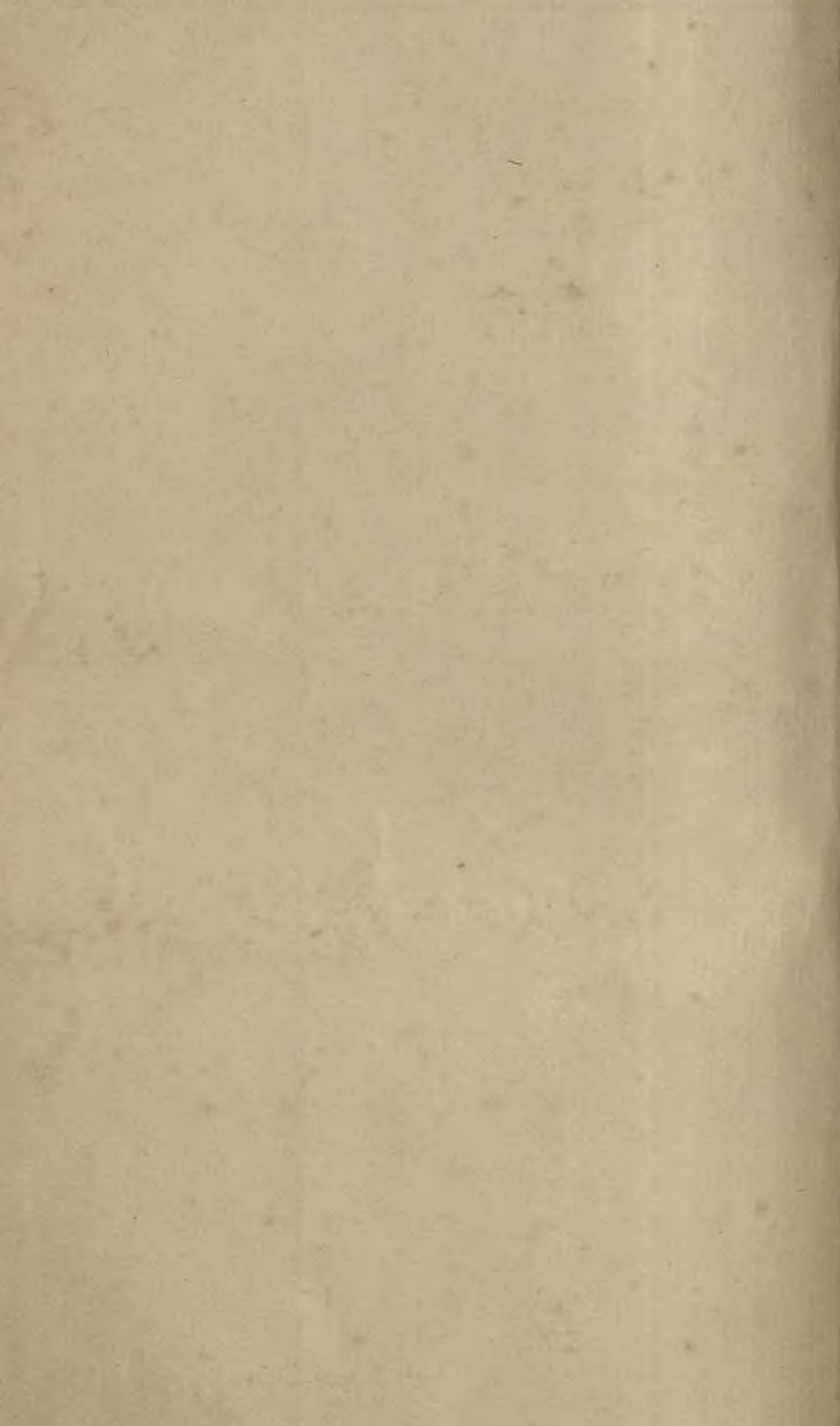


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GENERAL BOTANY

(VOLUME I)

7/52

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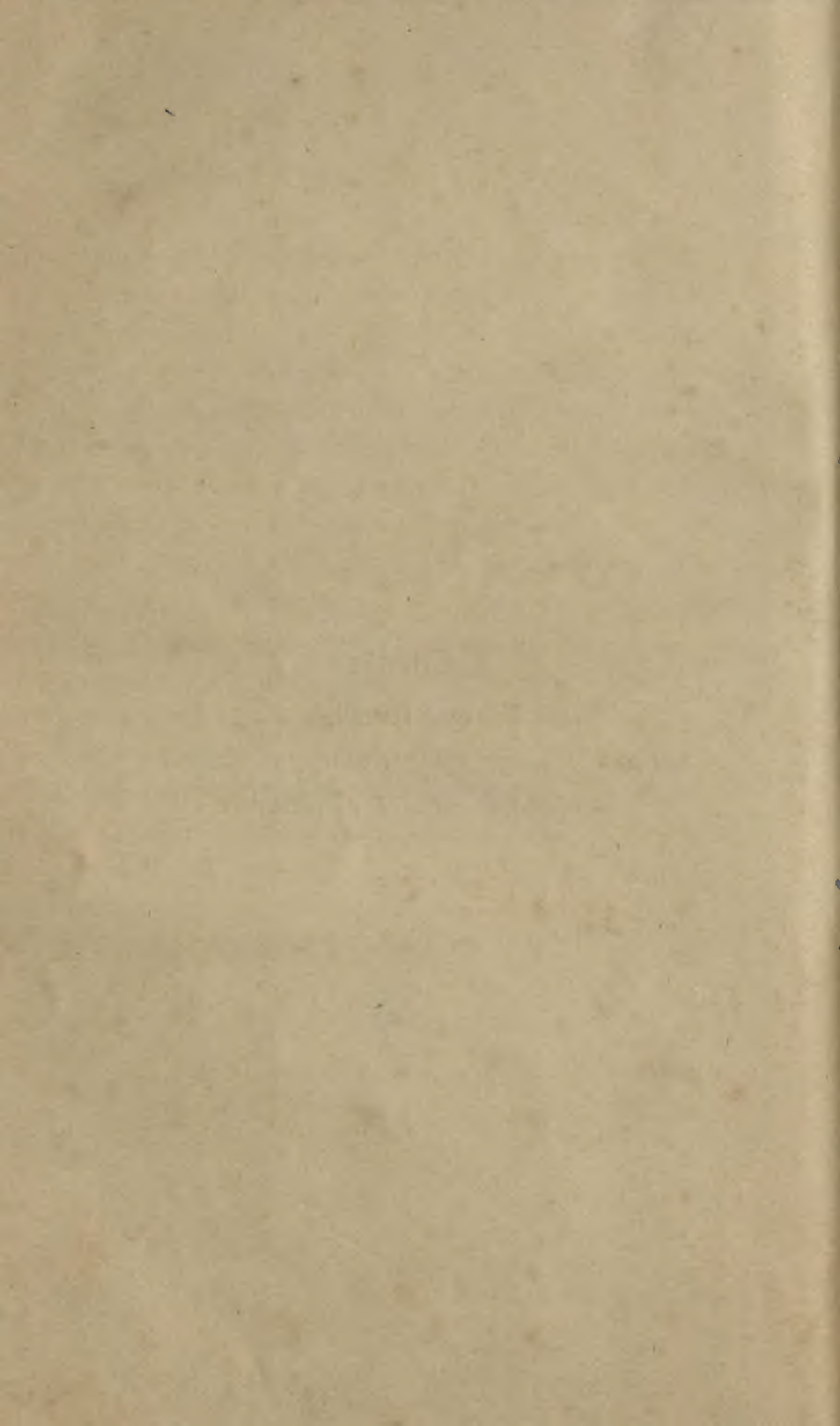
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who have made the teaching of Botany
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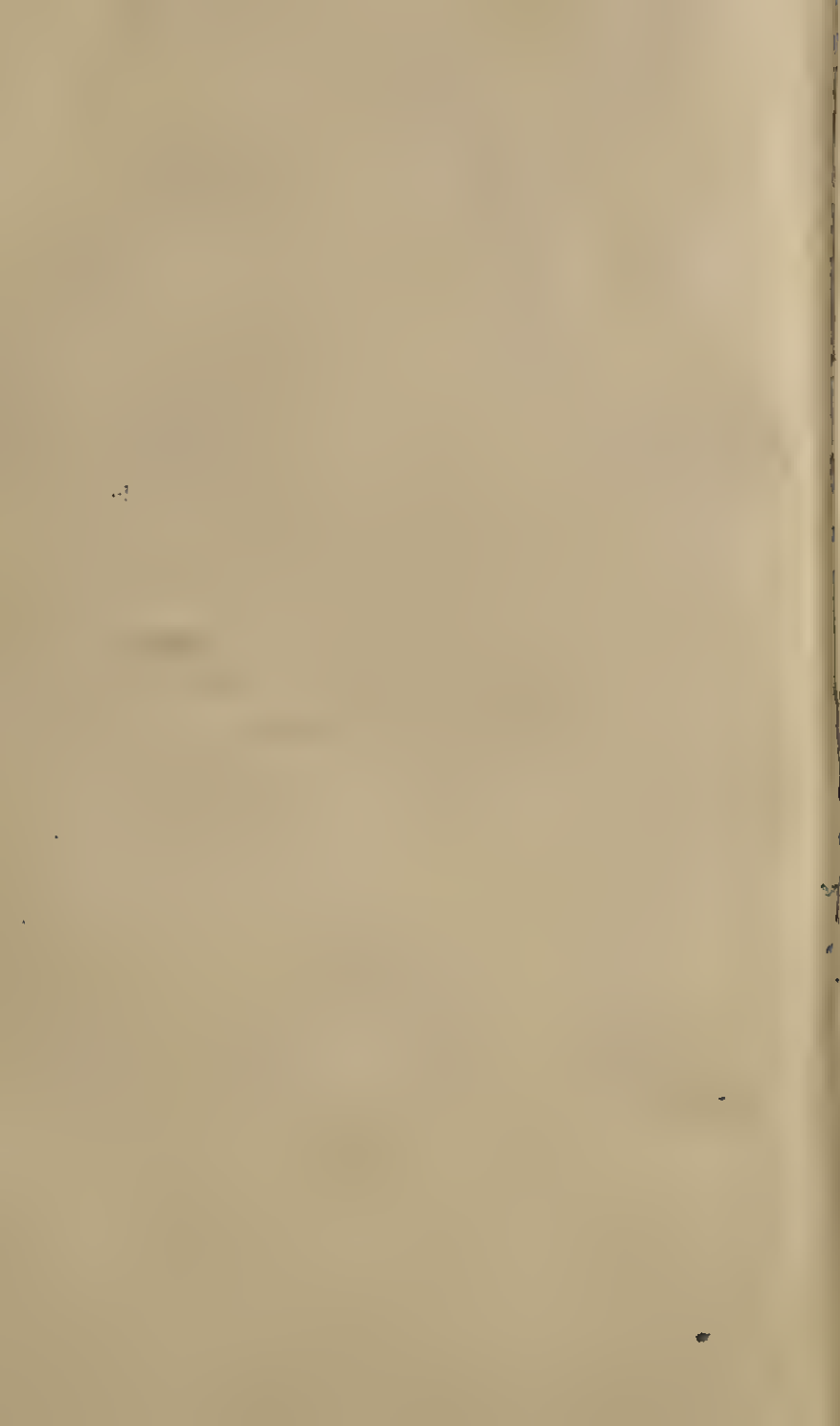


PREFACE TO THE FOURTH EDITION

We are indeed really happy in being able to present the fourth revised edition of "General Botany, Vol. I" to our beloved friends and students. As in the previous editions, the book has undergone a thorough revision. Consequently, some old matters and illustrations have been discarded with the incorporation of some newer ones. The most drastic changes have been brought about in the section dealing with the flower and the different cytological topics. In this connection, as before, we have freely consulted the standard and authoritative text-books on the various subjects, written both by Indian as well as foreign authors. For this, we remain grateful to them all. We are also indebted to a large number of friends of ours in different institutions, who have offered very valuable suggestions for the improvement of the book. Further, we should like to express our indebtedness to Profs. P. K. Pal and P. K. Mukherjee of City College, Calcutta, for their material contributions in the preparation of the text of some portions of the present volume. We hope that this revised edition will receive the same favour from teachers and students alike as its predecessors.

CALCUTTA
The 15th August, 1965.

H. M.
&
A. G.



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INTRODUCTION

The study of plants dates from very early periods, since apart from their manifold utilities, they form the ultimate source of food supply for the mankind as well as for the animals. Though the term 'Botany' has come from the Greek word *botane*, which means the herb, yet it is applied to the study of the vegetable kingdom in general. Of late, a newer term 'Phytology' is replacing the older one 'Botany', the word *phyton* meaning the plant.

Mankind got interested in the study of plant-life for the various uses of plants, some of which are enumerated below.

Our principal food is derived from plants. Like food, fuel is also obtained from plants. Wood is the universal source of heat. Coal, petroleum, and natural gases, although obtained from the earth, are the products of plants which lived in the past geological periods. The fibres for our clothing and other purposes are obtained from plants, such as cotton, flax, jute and hemp. Lumber, which is absolutely necessary for the construction of houses, buildings and furniture, as well as paper, the principal medium of communication and commercial exchange, are also essentially plant-products. Plants supply us with oils, fats, gums, resins, dyes, rubber, drugs, alcohols, the materials of explosives, etc. Trees and grasses on mountains and in valleys help to retain water and prevent destructive erosion. They also provide food and shelter for numerous wild animals of great economic importance. The plants of our lakes, ponds and streams are the chief sources of food and shelter for fishes, ducks and other aquatic animals. Green plants help in purifying the atmosphere by taking in the harmful carbon dioxide gas from it and giving out oxygen to it during the process of photosynthesis. Certain microscopic plants, like some algae, bacteria and fungi are beneficial in enriching the fertility of the soil by building nitrates and other nitrogenous compounds. Besides these, plants afford us an aesthetic pleasure, that cannot be measured in terms of money.

The present status of the study of Botany is mainly due to the efforts of the ancient philosophers, herbalists and amateurs through centuries. It is surprising to learn that there was a time when people, who were engaged in the study of plants, were regarded as harmless lunatics, and as such, were objects of pity. But, thanks God, that phase is over now, and gradually more and more people are leaning towards these handicrafts of Nature.

BOTANY AND ITS BRANCHES

Botany deals with the external and internal structures of plants, the methods of their growth and reproduction, their life-histories and economic importance, and their inter-relationships to one another. In other words, Botany studies plant-life from as many different points of view as possible, and is concerned with everything that has reference to plants. Like other sister sciences, the study of Botany is also divided into two branches : pure and applied. *Pure Botany* is concerned mainly with the academic side of the study of plants, while *Applied Botany* is closely connected with various commercial and economical aspects, like agriculture, horticulture, forestry, pharmaceuticals, brewing, bacteriology, plant breeding, soil conservation, etc.

For the convenience of study, the subject of Pure Botany has been mainly divided into the following important branches :

I. Morphology deals with the forms and structures of plant bodies, both *external* and *internal*, together with the relationships of the parts of plants to one another. *External morphology* deals with the studies of the external organs of plants. *Internal morphology* includes either the gross observation of the internal parts of plants or observation of their minute structures by means of a compound microscope ; the former is known as *anatomy*, and the latter, *histology*. Other important branches of Internal morphology are *cytology* (i.e., the study of the cell), *embryology* (i.e., the study of the modes of development of the different types of embryo), etc.

II. Physiology is concerned with the various life processes of plants and the functions of the different organs.

III. Systematic Botany includes (a) *classification* or the arrangement of different kinds of plants according to some definite system, (b) *taxonomy* or the principles of classification, based on the facts observed with their interpretation, and (c) *nomenclature* or the principles and rules adopted for assigning plant names.

IV. Ecology is the science of study of plants in relation to their environment.

V. Phytogeography or Plant Geography is the study of the distribution of plants over the surface of the globe.

VI. Economic Botany deals with plants of economic importance.

VII. Phytopathology or Plant Pathology deals with the diseases of plants and their remedies.

VIII. Palaeobotany or Fossil Botany is concerned with the study of plants of the past geological periods.

IX. Plant Genetics is the study of heredity in plants.

X. Organic Evolution deals with the various kinds of changes taking place in the plant kingdom, ultimately giving rise to new types of plants or causing total extinction of some of the types.

CLASSIFICATION OF PLANTS

There are about 4,00,000 different species of plants scattered all over the world in different habitats, and it is no easy task to make a systematic study of all of them without following some definite system or principle. Though ancient Indians had studied plants chiefly from the medicinal point of view, of which records are to be found in the *Upanishadas*, yet the real attempt for the classification of plants began with the classical work (*The Enquiry into Plants*) of Theophrastus (370 to 285 B.C.), a Greek philosopher. Later on, in the 16th century, herbalists, like Brunfels, Fuchs, and others, made valuable contributions towards the study of Systematic Botany. In the 18th century remarkable achievements were made in this line by the immortal Swedish botanist, Linnaeus. Later on, workers, like Jussieu, De Candolle, Bentham and Hooker, Eichler, Engler and Prantl,

Hutchinson, Tippo and others, have propounded different systems of classification from time to time, each having its own merits and demerits. For the sake of convenience for the beginners, the system of Bentham and Hooker, as published in the *Genera Plantarum*, has been presented in the following lines.

Of the different kinds of plants, some bear seeds, while the rest are without them. The *Plant Kingdom* is, therefore, broadly classified into two sub-kingdoms : *Cryptogamia* (flowerless or seedless plants) and *Phanerogamia* (flowering or seed-bearing plants).* The former are simpler in body-construction than the latter.

CRYPTOGAMIA have been further sub-divided, according to the complexity of structure, into three divisions :

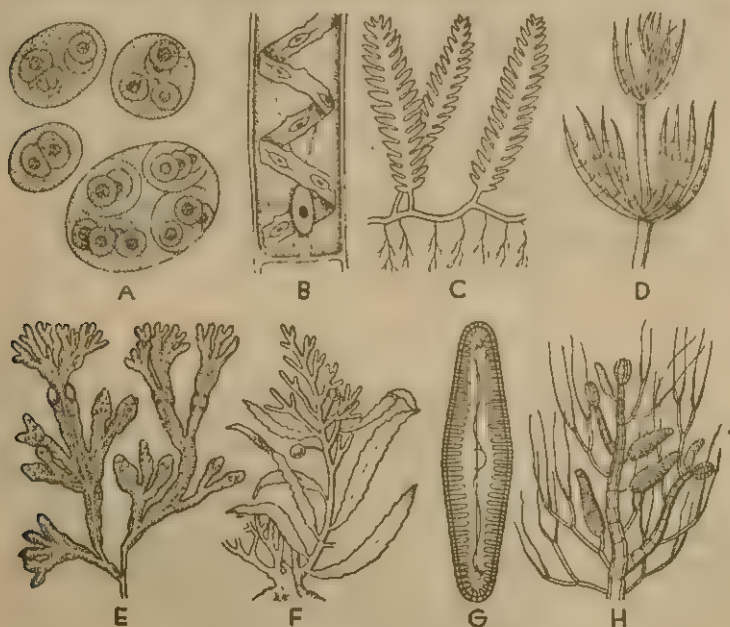


FIG. 1. DIFFERENT TYPES OF ALGAE.

A, *Gleocapsa* ; B, *Spirogyra* ; C, *Caulerpa* ; D, *Chara* ; E, *Fucus* ; F, *Sargassum* ; G, a diatom ; H, *Polysiphonia*.

*It is interesting to note, however, that these terms are rather misnomers. Because, in *Cryptogamia* (*cryptos*—hidden ; *gamos*—sexual union or marriage), the sexuality is more evident than in *Phanerogamia* (*phaneros*—evident). As such, the present-day systems of classification are mainly based on the presence or absence of seeds.

(a) The first and lowest of these divisions is the **Thallophyta**. They are the simplest of all plants, since their body cannot be differentiated into organs like root, stem and leaf, and such an undifferentiated plant body is called a **thallus**. The thallus body may be built up of one cell only (unicellular) or of many cells (multicellular), and the sex organs are in general unicellular. The thallophytes again, according to the mode of their life-process, are mainly divided into four sub-divisions : algae, fungi, bacteria, and lichens. (1) *Algae* (Fig. 1) are usually green in colour, which is due to the presence of a pigment, known as *chlorophyll*. In the higher forms of algae there is a progressive differentiation of the thallus body into organs resembling root, stem and leaf. The

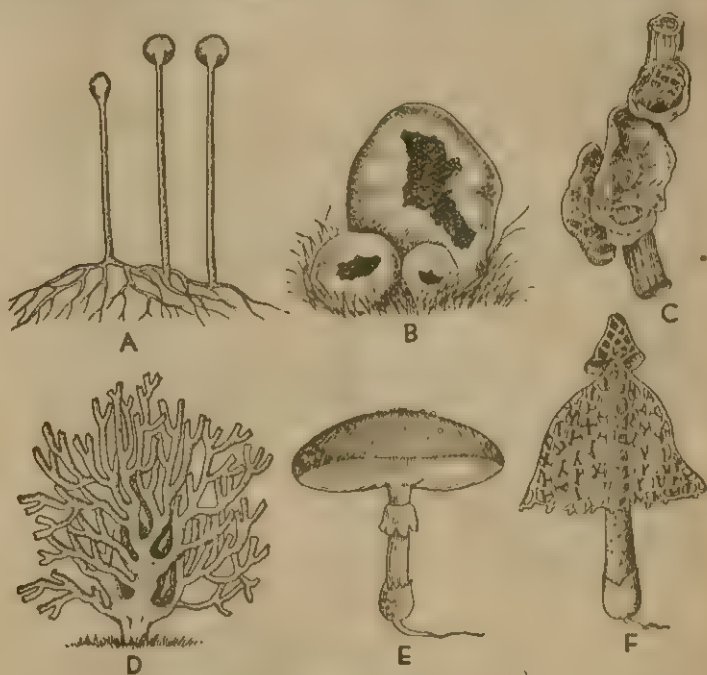


FIG. 2. DIFFERENT TYPES OF FUNGI.

A, *Mucor* ; B, *Peziza* ; C, *Auricularia* ; D, *Clavaria* ; E, *Amanita* ; F, *Dictyophora*.

green scum on wet grounds or on the surface of ponds are the commonest examples of algae. The fresh-water algae are mostly green or blue-green, and the marine ones, which constitute the

seaweeds, are mainly red or brown. The algae, by virtue of their possessing the green pigment, chlorophyll, are capable of manufacturing their own food and are, therefore, called **autophytes**. The different kinds of algae are used for various commercial and industrial purposes, like insulation of boilers, manufacture of abrasives, preparation of kelp, agar, *etc.*, filtration of water, preparation of food-stuffs, and others. (2) *Fungi* (Fig. 2) are non-green thallophytes and are characterized by the total absence of chlorophyll, and as such, they cannot prepare their own food. They, therefore, live either as parasites on living organisms, or as saprophytes on dead and decayed vegetable or organic materials, and are known as **heterophytes**. The common moulds,

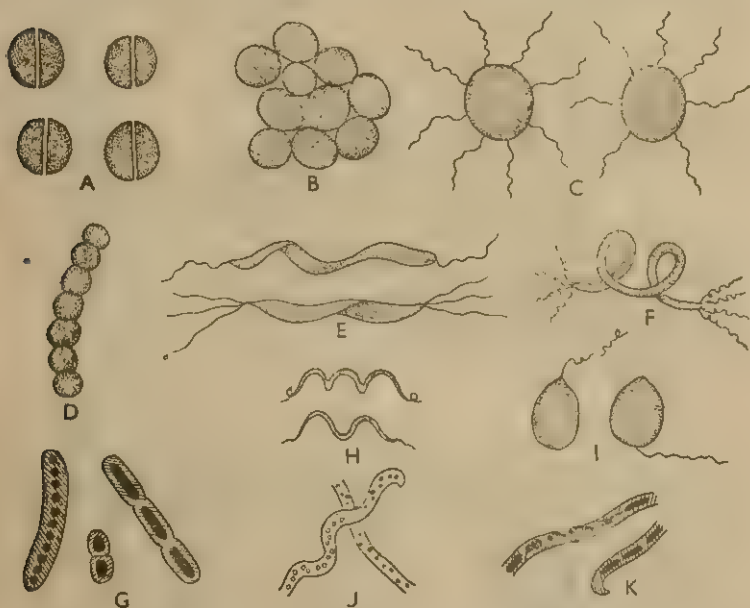


FIG. 3. DIFFERENT TYPES OF BACTERIA.

A, *Diplococcus* ; B, *Staphylococcus* ; C, *Bacillus typhosus* ;

D, *Streptococcus* ; E, *Spirillum* ; F, *Rhizobium* ; G, capsulated bacteria ;

H, *Spirochaete* ; I, *Vibrio* ; J, sulphur bacteria ; K, iron bacteria.

which are very prevalent on stale bread, moist leather, preserved fruits, jams, jellies and pickles, *etc.*, as well as the puffballs, mushrooms and toadstools, are familiar examples of fungi. Though the majority of fungi are, as a rule, destructive in nature, yet some of them are extremely useful, as they yield very valuable

drugs, while some are used as food. (3) *Bacteria* (Fig. 3) are non-chlorophyllous unicellular micro-organisms, leading a saprophytic mode of existence. They may be pathogenic, causing serious damages and even destruction to the plants and animals, or non-pathogenic, some of which are highly beneficial. (4)

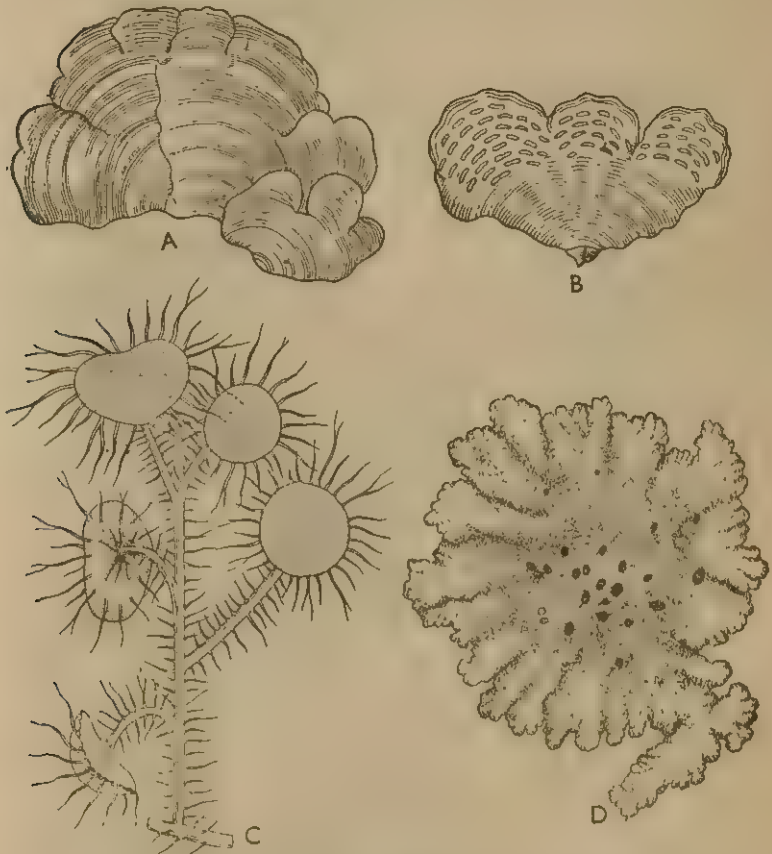


FIG. 4. DIFFERENT TYPES OF LICHENS.
A, *Cora pavonia* (dorsal view) ; B, the same (ventral view) ; C, *Usnea* ;
D, *Physcia*.

Lichens (Fig. 4) are specialized organisms, composed of two heterogenous partners, one of which is an alga and the other a fungus, living in a close symbiotic association. The fungus is mildly parasitic upon its algal partner, which is capable of

manufacturing food ; on the other hand, the fungus is supposed to help the alga in its absorption as well as retention of water. The lichens are chiefly found on the bark of trees, different types of soils, and on rocks. In some parts of the world, these are used as human food, as well as food for the domesticated animals. Some of them are extensively utilized in the manufacture of dyes, soaps and perfumes, and for various other commercial and industrial purposes.

(b) **Bryophyta** (Fig. 5), which have more complex structure of the plant body than the thallophytes, comprise the second division. The plant body of a bryophyte is usually differentiated



FIG. 5. DIFFERENT TYPES OF BRYOPHYTES.

A, *Marchantia* ; B, *Lejeunea* ; C, *Anthoceros* ; D, *Pogonatum*.

into stem and leaf-like organs, but does not possess any true root, e.g., the liverworts and mosses. Amongst the former, one notices a progressive complexity of structure from the thallose to typical foliose forms. The members of this division are usually found living in moist, shady places, and are of little economic importance.

(c) **Pteridophyta** (Fig. 6) constitute the third and highest group of cryptogamic plants. Their body is completely differentiated into root, stem and leaves. But, they differ from the higher plants (Phanerogams) in that they do not possess any seed. The ferns, horsetails, lycopods, etc., are familiar examples.* They

*Both Bryophyta and Pteridophyta possess many-celled sex organs, in each of which there is always a jacket of sterile cells, and unlike that in the Thallophyta, the zygote develops into a multicellular embryo, while still inside the female sex organ.

are chiefly found in moist, shady places. Since they possess a well-differentiated vascular system, they are also known as the **Vascular Cryptogams**. Some of the ferns are edible, while in general, the fossil members of this division contribute extensively to the formation of coal.

PHANEROGAMIA, on the other hand, include those plants which show complete differentiation of the plant body into root, stem and leaves, like the Pteridophyta, but in addition to these



FIG. 6. DIFFERENT TYPES OF PTERIDOPHYTES.

A, *Lycopodium* ; B, *Selaginella* ; C, *Equisetum* ; D, *Dryopteris* (a fern).

organs, they produce flowers and seeds. They have been divided into two divisions :

(a) **Gymnospermia** or naked-seeded plants (Fig. 7) are those, whose seeds remain naked or exposed, and are not enclosed within a fruit. The majority of these are big trees. The pines, firs, larches, cycads, etc., belong to this group. The majority of them are good sources of timber. Some yield charcoal, tar, various kinds of oil, turpentine, methyl alcohol, tannin, and valuable alkaloid (like ephedrine). while others are used in the

manufacture of ink, paper, drugs, etc. The fossil members contribute to coal formation.



FIG. 7. DIFFERENT TYPES OF GYMNASPERMS.

A, *Cycas* ; B, *Pinus* ; C, *Gnetum* ; D, *Ephedra* ; E, *Ginkgo*.

(b) **Angiospermia** or closed-seeded plants (Fig. 8) are those, whose seeds are enclosed within the fruits. The Angiospermia are further divided into two co-ordinate classes : (i) *Dictyyledonae*, and (ii) *Monocotyledonae*. The former comprises of those plants, in which the embryo within the seed contains two cotyledons or seed-leaves, such as mangoes, peas, pulses, and many others, while the latter includes those plants, in which the embryo has only one cotyledon, such as grasses, bamboos, bananas, orchids, various cereals, etc. The economic importance of the angiosperms is

manifold. The utilities of the different organs of some of them have been briefly discussed later on.

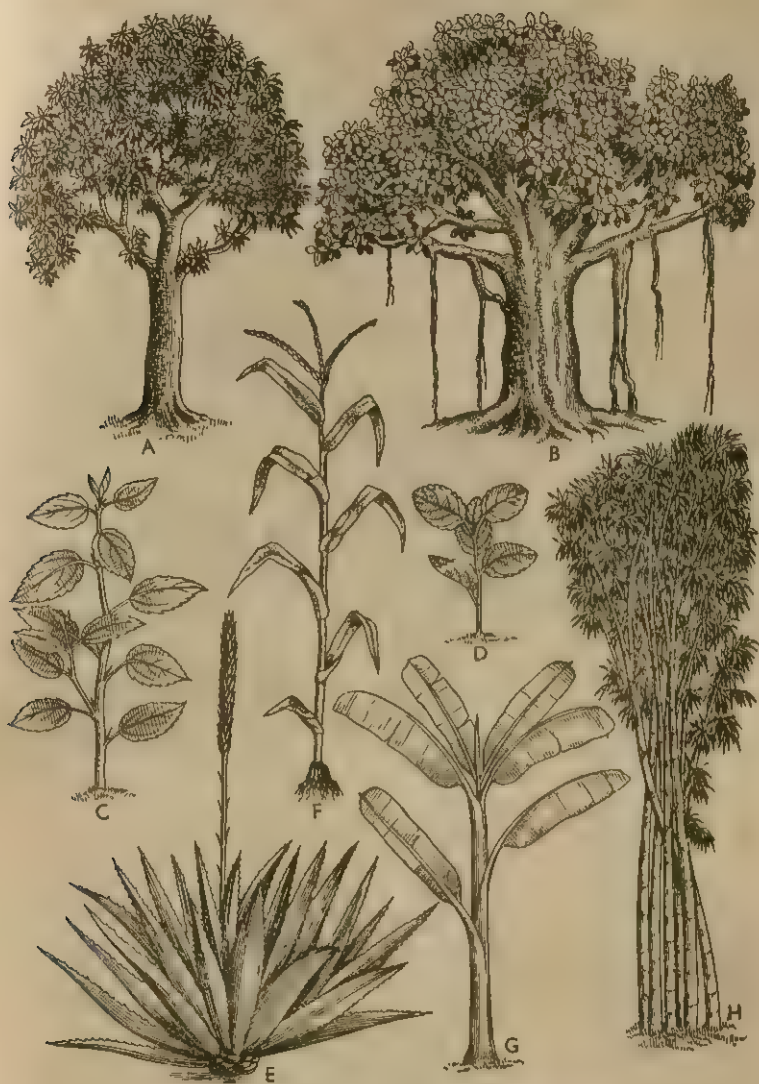


FIG. 8. DIFFERENT TYPES OF ANGIOSPERMS.

A, Mango ; B, Banyan ; C, Tea ; D, Tobacco ; E, Agave ; F, Maize ;
G, Banana ; H, Bamboo.

As one proceeds from the thallophytes to the angiosperms, two important points are noticed : the gradual evolution in the complexity of structure of the plant body including the establishment of a well-differentiated vascular system, and a migration of plants from water to land. In this sense, the bryophytes occupy an intermediate position, that is, like the frog in the animal kingdom, they are amphibious in habit. Further, the *alternation of generations* becomes fully evident with a gradual ascendancy of the sporophytic generation over the gametophytic one.

According to their *modes of nutrition*, plants may be classified into two groups :

I. **AUTOPHYTES** are those plants which possess the green pigment, chlorophyll, by means of which they are able to manufacture their own food from inorganic salts and water derived from the soil, and carbon dioxide obtained from the atmosphere, in presence of light. The common green plants and epiphytes are examples of autophytes.

Epiphytes or air plants remain attached to other plants - mainly deriving mechanical support, but not drawing food



FIG. 9. EPIPHYTES.
A, *Vanda roxburghii* ; B, *Dischidia rafflesiana*.

from them like the parasites. These plants live friendly with the host plants and adopt various contrivances for obtaining the

atmospheric moisture as well as rain water, since they are entirely cut off from the surface of the soil. The epiphytes are usually characterized by their water-storing arrangements or by their mode of absorbing water. Many epiphytic orchids (e.g., *Vanda roxburghii*, Fig. 9, A, and *Dendrobium*) and aroids develop a special water-absorbing tissue (**velamen**) on the surface of the aerial root and absorb moisture from the atmosphere; the velamen also acts as a water-reservoir. In case of some other epiphytic orchids, aroids and ferns (like *Asplenium nidus*), some receptacles are formed by the leaves or aerial roots. Within these receptacles humus or other materials are collected, which act as reservoirs of water in a sponge-like manner, while the absorbing roots derive their nourishment from these moist compost-like masses*. The epiphytic members of the family Bromeliaceae, excepting *Tillandsia usnioides*, possess a short axis bearing a rosette of sessile leaves with prominent sheathing bases; the closely overlapping edges of these sheaths encircle the axis, and collectively form a pitcher or cistern in which rain water, dead bodies of insects, bits of decaying leaves, etc., are collected. The water and dissolved substances are absorbed by peculiar peltate hairs developed on the inner surfaces of the sheaths. In *Dischidia rafflesiana* (Fam. Asclepiadaceae, Fig. 9, B) the mechanism for a constant supply of water is beautifully exhibited by the formation of pitcher-like structures by the leaves, inside which rain water is collected, and this is absorbed by the much-branched adventitious roots developed from the nodes where the pitchers are developed.

II. **HETEROPHYTES** are those plants which may or may not contain chlorophyll, but their modes of nutrition are quite different from those of the autophytes. These are of the following four types† :

(a) **Parasites** (Fig. 10) are those plants, which derive nourishment from other living plants and animals, called the **hosts** or **suscepts**. An angiospermic parasite usually confines itself

* Besides these aerial and absorbing roots, the epiphytic orchids possess negatively phototropic (*vide* Part II, Vol. II), clinging roots, which become very closely attached to the substratum.

† Examples in these cases are mainly cited from the phanerogams, excluding the cryptogams, which contain a large number of heterophytes.

exclusively to the root (a **root-parasite**) or to the stem (a **stem-parasite**) of the host. There is a close relationship between the host and the parasite. Sometimes the parasites may be wholly dependent on the hosts, and are known as **holoparasites** or **total parasites**, as in *Balanophora dioica* (a leafless root-parasite and without any chlorophyll) of Fam. Balanophoraceae (Fig. 11), *Orobanche caryophyllacea* (a root-parasite, herb, containing little



FIG. 10. PARASITES.

A, *Cuscuta reflexa* ; B, *Viscum album* ; C, *Loranthus longiflorus* ;
D, *Orobanche caryophyllacea* ; E, *Cassytha filiformis*.

or no chlorophyll) of Fam. Orobanchaceae (Fig. 10, D), *Rafflesia arnoldi** (a root-parasite, occasionally stem-parasite, herb, with

* In *R. arnoldi* the flowers are about a yard in diameter.

colossal flowers) of Fam. Rafflesiaceae (Fig. 12), *Cassytha filiformis* (a stem-parasite, thread-like herb) of Fam. Lauraceae (Fig. 10, E), dodder (*Cuscuta reflexa*, a stem-parasite, thread-like twiner) of Fam. Convolvulaceae (Fig. 10, A), *Arceuthobium minutissimum* (a stem-parasite, the smallest dicotyledonous plant) of Fam. Loranaceae, and others. In other cases they are **partial parasites** or **semi- or hemi-parasites**, deriving a considerable portion of their nourishment from the host plants, but are also capable of manufacturing a part of their own food, as they possess green leaves. The mistletoes (*Viscum album*, Fig. 10, B and *Loranthus*

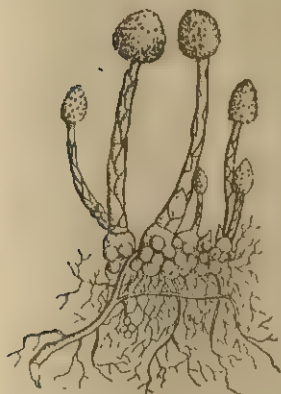


FIG. 11. *Balanophora dioica*.

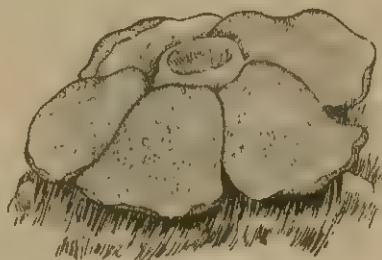


FIG. 12. *Rafflesia arnoldi*.

longiflorus of Fam. Loranaceae (Fig. 10, C), hemiparasitic herbs on branches of trees, sandal wood (*Santalum album*, a root-parasite belonging to Fam. Santalaceae), and others afford common examples. The relationship between the total parasites and the host plants is one of direct hostility, culminating in the death of the host. For instance, valuable forest trees supplying wood are often destroyed by the attack of different kinds of parasites. Special structures associated with the drawing of nutrition are the **haustoria** (root-suckers) or parasitic roots, which penetrate into the bodies of the hosts and establish connections

with their food-conducting channels robbing them of their prepared food and often killing them in the process.

(b) **Saprophytes** are those plants which obtain their food material entirely from dead plant or animal remains and decayed organic matters. These are sharply contrasted with the autophytes as well as with the parasites regarding the nature of their food, which is organic. Like the parasites, they may be classified into **holosaprophytes** and **partial saprophytes**, according to their entire or partial dependence on the substrates for the supply of food matters. Examples of holosaprophytes can be cited from the fungi and bacteria. *Monotropa uniflora* (a leafless saprophyte, living on moist humus in thickets) of Fam. Pyrolaceae (Fig. 13), *Andruris* sp. (Fam. Triuridaceae), *Burmannia* sp. (Fam. Burmanniaceae), a few orchids (*Neottia* sp.,



FIG. 13. SAPROPHYTE. *Epipogon* sp., *Limodorum* sp., *Corallorhiza* sp., etc., some members of the family Gentianaceae (like *Obolaria* sp., *Bartonia* sp., etc.), prothalli of some ferns (*Botrychium*, *Helminthostachys* and *Ophiglossum*,—all belonging to Fam. Ophioglossaceae), and others also afford good examples of saprophytes among higher plants. The saprophytes do not usually develop such structures that are not required for their special mode of life; reduced output of chlorophyll-containing bodies as well as reduced development of roots and root-like structures characterize these plants.

(c) **Symbionts.** When two different organisms live in close association and derive mutual benefit, they are called **symbionts**, and the condition is known as **symbiosis**. The best examples are afforded by the lichens. A special case of symbiosis is noted in some of the leguminous plants, whose roots harbour nitrogen-fixing bacteria. Another special type of symbiosis is known as **mycorrhiza** (also spelt as *mycorrhiza*), where a fungal mycelium is found to live in the root of a higher plant. In such cases, the hyphae carry on the function of absorption of nutrients from the substratum, and thus can be regarded as replacing the root hairs.

(d) **Insectivorous or carnivorous plants** (Fig. 14) are those, which obtain their nourishment partly from insect-bodies. These plants are provided with special entrapping organs, which are remarkable adaptations of leaves meant for capturing insects and securing nitrogen from their bodies. The insectivorous



FIG. 14. INSECTIVOROUS PLANTS

A, *Nepenthes khasiana* ; B, *Utricularia stellaris* ; C, a bladder of the same (in sectional view) ; D, *Drosera burmanni* ; E, a leaf of the same ; F, *Aldrovanda vesiculosa* ; G, a leaf of the same.

plants are either rootless or have a weakly-developed root system. They are chiefly found in localities where the soil is deficient

in nitrogenous contents essential to plant life. Some are found in bogs containing abundant decomposed organic substances. The best-known insectivorous plants of India are (1) pitcher plant (*Nepenthes khasiana*) of Fam. Nepenthaceae, common in the wet districts of Assam, (2) bladderwort (*Utricularia stellaris*) of Fam. Lentibulariaceae, commonly found in old tanks, (3) sundew (*Drosera burmanni*, *D. indica*, *D. rotundifolia*), a common weed of paddy fields in some localities, and (4) Venus' fly trap (Malacca jhanji or *Aldrovanda vesiculosa*) of Fam. Droseraceae, a submerged herb of salt lakes. For detailed discussions on these plants refer to Vol. II, Part II.

It should be noted that besides the above-mentioned insectivorous plants, there are some others, like the genera *Sarracenia*, *Darlingtonia*, *Heliamphora*, *Cephalotus*, *Pinguicula**, *Dionaea*, *Drospophyllum*, etc., growing in different parts of the world, but these are not found in India.

PARTS OF AN ANGIOSPERMIC PLANT (Fig. 15)

On examining any common angiospermic plant, one notices that it normally consists of two main parts : (1) the **root system**, the underground portion, and (2) the **shoot system**, the subaerial portion. The root system usually consists of a main axis, the **tap root**, which bears secondary and tertiary similar lateral members, the **branch roots**, in acropetal order of succession, i.e., the youngest branch is nearest to the growing tip and the oldest one is further away from it. The shoot system, on the other hand, consists of a main axis, the **stem**, which bears similar and dissimilar lateral members, the **branches** and the **leaves** respectively, also in acropetal order. The stem or its branch is usually differentiated into **nodes** (places from which leaves develop) and **internodes** (regions between any two consecutive nodes). Besides these, each leaf subtends usually one **bud** (condensed shoot), called the **axillary bud**, in its **axil** (the angle which the upper surface of the leaf makes with the stem). The main axis as well as each of its branches terminate in a bud, known as the **terminal bud**. At the proper season, the shoot bears flowers, fruits and seeds. Each part of the plant has a definite work to perform and

*One species of *Pinguicula*, *P. alpina*, is, however, reported to be found in the alpine Himalayas.

this work is known as its *function* ; the various parts (considered before), from functional point of view, are regarded as **organs of vegetation** or **vegetative organs**, since they are usually necessary

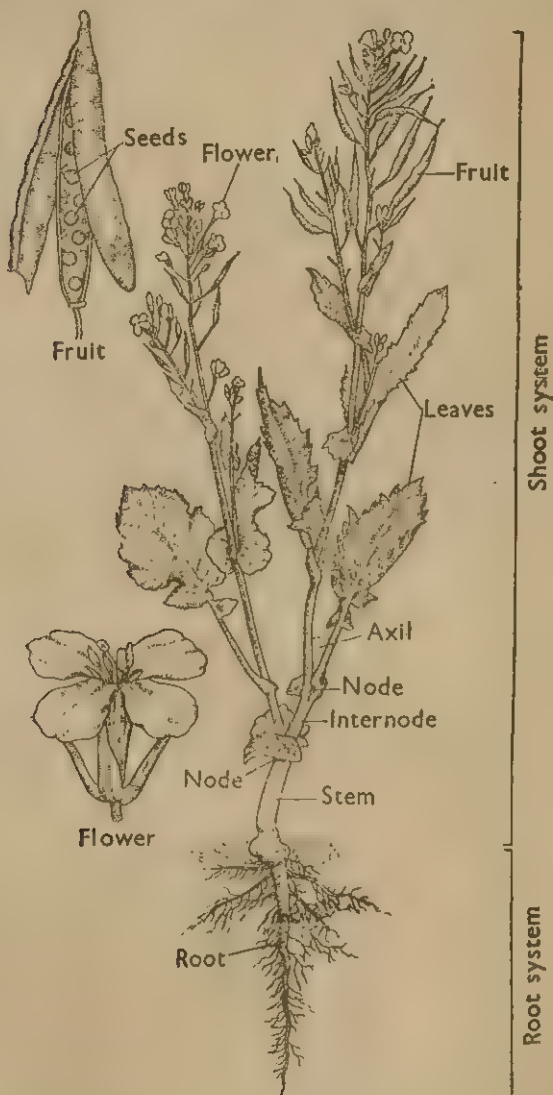
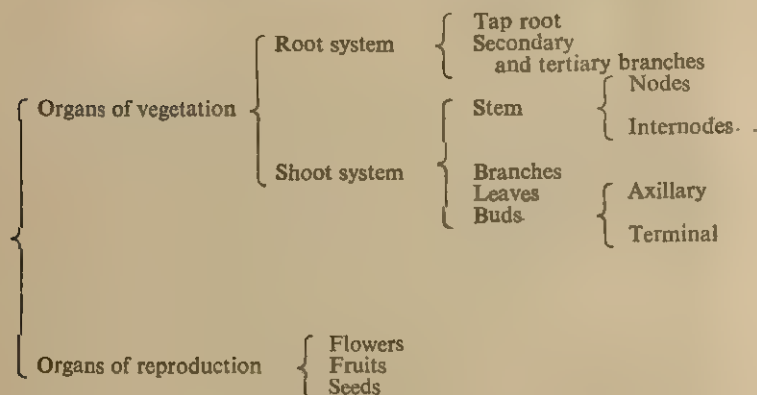


FIG. 15. PARTS OF AN ANGIOSPERMIC PLANT
(*Brassica nigra*).

for the growth of a plant, and the other parts, viz., **flowers, fruits*** and **seeds**, are concerned with its multiplication, and hence regarded as **organs of reproduction or reproductive organs**.

The parts of a typical seed plant may be tabulated as follows :



*Strictly speaking, the fruit should not be regarded as an actual organ of reproduction. Under some special circumstances, roots, stems and leaves may also act as reproductive organs.

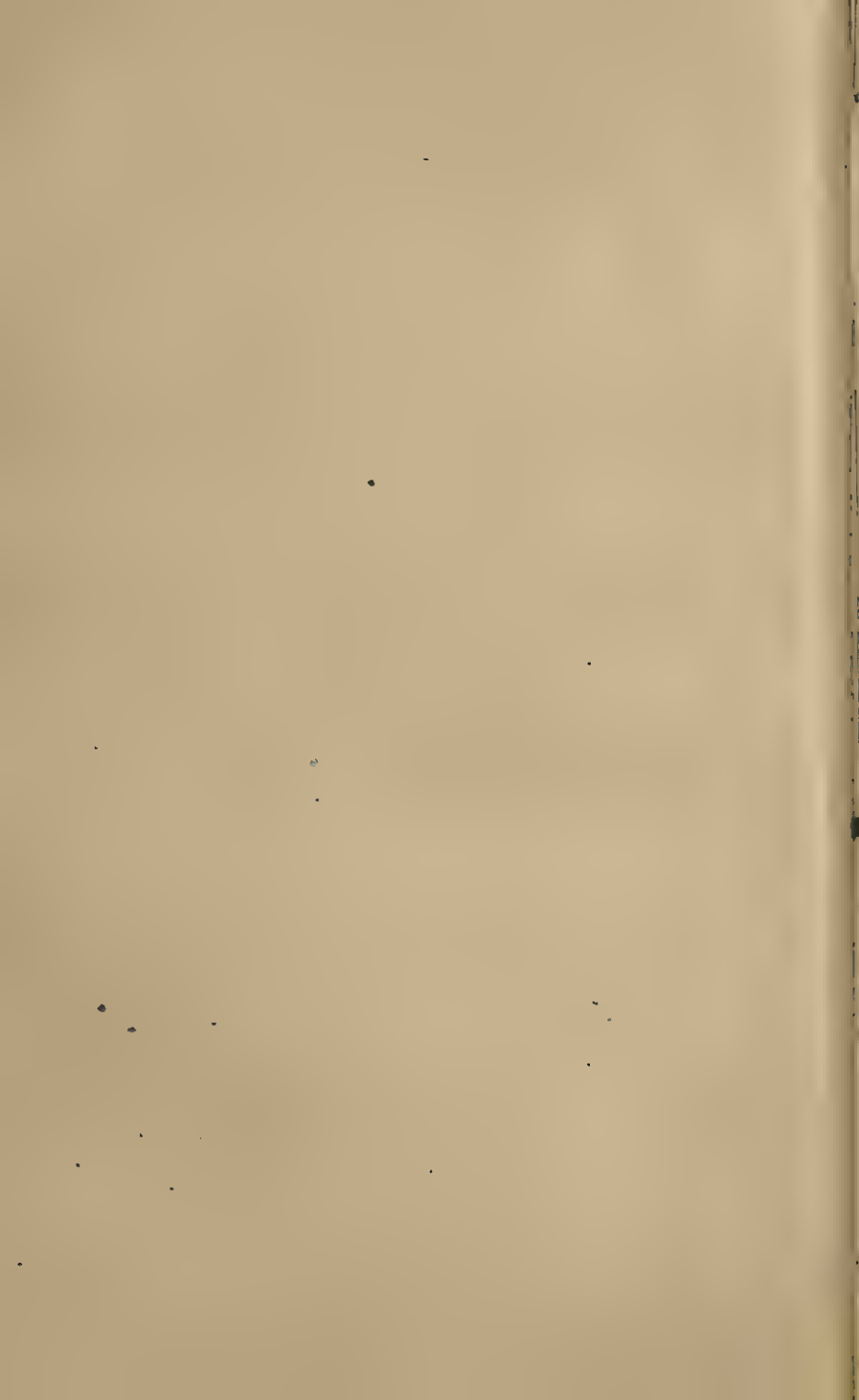
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PART I
MORPHOLOGY

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CHAPTER I

THE ROOT

The root is the descending axis of the plant body. It is normally derived from the radicle, and in most of the dicotyledonous plants, it makes its way straight down into the soil forming the main **primary root**, which usually persists, and sends off similar lateral members, the **secondary** and **tertiary branch roots** in oblique and acropetal fashion. These go on ramifying into smaller and smaller branches or rootlets, eventually producing an elaborate **true or tap-root system** (Fig. 16). But in the majority of monocotyledonous plants, the primary root either dies down early, or its growth is soon arrested, and there arises



FIG. 16. TAP-ROOT SYSTEM



FIG. 17. FIBROUS ROOT SYSTEM

from the base of the shoot a cluster of **fibrous roots**, so that the tap root is entirely absent in these plants. Consequently, the roots, in such cases, form a **fibrous root system** (Fig. 17). The branching in such fibrous roots is also not vigorous. Sometimes,

plants are entirely rootless. Besides the thallophytes and the bryophytes, some aquatic pteridophytes (e.g., *Salvinia natans*, *S. cucullata*, etc.), and angiosperms, e.g., water milfoil (*Myriophyllum indicum*) of Fam. Haloragidaceae, bladderwort (*Utricularia stellaris*) of Fam. Lentibulariaceae, *Wolffia arrhiza* of Fam. Lemnaceae, *Epipogum* sp. (Fam. Orchidaceae), and some others are also lacking in roots. On the other hand, plants like *Monotropa uniflora* (Fam. Pyrolaceae), and members belonging to the family Podostemaceae have vegetative bodies mainly composed of roots.

CHARACTERISTIC FEATURES

As the roots and stems normally live in two entirely different environments, they have different functions to discharge. Their

morphological features are, consequently, different. The roots have the following distinctive morphological characteristics.

Roots are usually not green, and are almost conical in shape, gradually tapering from the base towards the free end, i.e., the apex, and form the descending axis of the plant. In most cases, they tend to grow away from the direction of light (negatively phototropic), go straight down into the soil (positively geotropic) seeking water

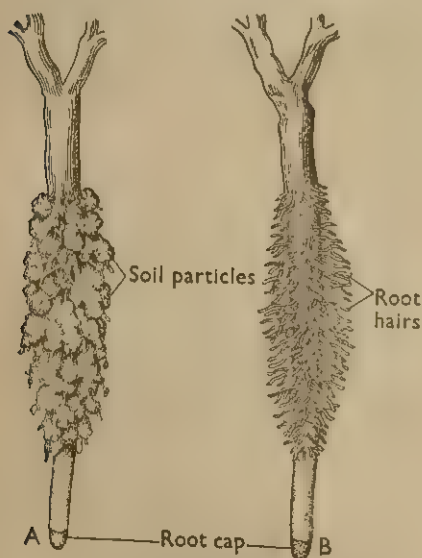


FIG. 18. ROOT HAIRS

A, Root hairs with soil particles ; B, The same with the soil particles removed.

(positively hydrotropic), and fixing the plant to the substratum. They are neither divided into nodes and internodes, nor do they bear leaves, leaf buds and flowers, exceptions being found only in very few cases. The branches are endogenous in origin. The growing tip is normally protected by a special protective

structure, known as the **root cap** or **calyptra**. The root cap may be either **simple**, as in *Amaryllis* sp. of Fam. Amaryllidaceae (Fig. 19, A), *Ficus* sp. (Fam. Moraceae), etc., or **multiple**, as in screwpine (*Pandanus foetidus*) of Fam. Pandanaceae (Fig. 19, B). As the root grows, the old root cap withers away, and a new one is developed. The functions of the root cap

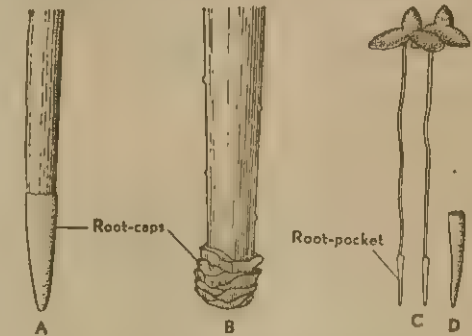


FIG. 19. ROOT CAPS AND ROOT POCKETS
A, Simple root cap ; B, Multiple root cap ; C, Root pocket ; D, Enlarged view of the same.

are to afford protection to the delicate root tip and guidance to the root through the soil containing various inorganic salts in a watery solution. During growth, when the root forces its way through the soil, the outer surface of the root cap becomes gelatinous, and secretes a slimy substance, which minimizes its friction with the soil particles. At a short distance back from the tip is a region provided with fine delicate hairs, called **root hairs** (Fig. 18). As the root grows, new root hairs (which are unicellular living cells, and are exogenous in origin) continually appear towards the tip, while the older ones gradually die and disappear. In case of not coming in contact with any solid obstacles, the root hairs usually come out at right angles to the longitudinal axis of the root. Inside the soil, however, they may assume any shape depending on the shape and size of the soil particles, which they encounter in course of their journey. The root hairs normally live for a few days only. In exceptional cases, they persist for a few months, and in some members of the family Compositae, they are known to live for about three years. As regards functions, they are the main organs for absorption of raw food materials in a watery solution from the soil. They are also partly responsible for fixation of the plant to the soil, as they can firmly cling to the soil particles.

In some cases, as in water lettuce (*Pistia stratiotes*) of Fam. Araceae, duckweed (*Lemna trisulca* of Fam. Lemnaceae, Fig.

19, C & D), *etc.*, a root-cap-like structure, known as the **root pocket**, is developed at the growing tip of the root. The root pocket, unlike the root cap, does not arise from the epiblema of the root, and does not show periodic renovation. In the form of a loose thimble or the finger of a glove, it protects the root apex against the attacks of small animals, the effects of currents of water and the like.

The root bears the impress of its environment or the medium in which it grows. The aquatic roots do not usually bear root hairs, and contain abundant air-spaces. The epiphytic roots develop a special kind of absorbing sheath (**velamen**) on their aerial roots. The desert plants either have a superficial root system to absorb any chance atmospheric precipitation or a deep-seated root system, so that they can get their supply of water situated in the deeper layers of the soil. The roots of plants growing in salt marshes send characteristic breathing roots into the air. Thus, plants living in different conditions of life have different adaptations in their roots.

According to their structure and mode of development, roots may be classified as *primary*, *secondary*, and *adventitious*.

The **primary root** is the direct prolongation of the radicle, which usually grows downwards. It is the first-formed root of the plant ; in many cases, it persists throughout the life of the plant as the main root, and becomes stouter than its branches, when it is called the **tap root**.

The branches developed from this primary root are known as **secondary roots**. Sometimes, branch roots originating from the secondary roots are termed as **tertiary roots**, but all the branches from the primary root may be collectively called secondary roots. Secondary roots develop at a considerable distance from the root apex, and they are endogenous in origin, *i.e.*, they take their origin from an inner tissue, called the pericycle.

All the other roots, which are neither developments of the radicles, nor are branches of the primary root, are called **adventitious roots**. They may arise from any other part of the plant body, *viz.*, (1) from stems, as in maize (*Zea mays*), sugarcane (*Saccharum officinarum*), bamboo (*Bambusa arundinacea*) and other plants belonging to Fam. Gramineae, (2) from leaves,

as in *Begonia* sp. (Fam. Begoniaceae), *Bryophyllum calycinum* and *Kalanchoe laciniata* of Fam. Crassulaceae, etc. Adventitious roots also develop from the bodies of underground stems, as well as from the lower ends of stem-cuttings, as in pear (*Pyrus communis*) and rose (*Rosa centifolia*) of Fam. Rosaceae, China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, and others.

DIFFERENT REGIONS OF A ROOT (Fig. 20)

Whatever may be the nature of the root, true or adventitious, it is usually differentiable into a few regions or zones, each of which gradually merges into the other. Arranged in order from the apex towards the base of the root, these can be designated as the *root-cap zone*, the *meristematic zone* or *zone of cell division*, the *zone of cell enlargement*, the *zone of cell maturation*, and the *mature zone* or *zone of permanent tissues* (*primary and secondary*) ; the *root-hair zone* begins in the cell enlargement zone and extends up to the zone of the primary permanent tissues.

(i) **The root-cap zone**—This is found to occupy the extreme tip portion of the root. Excepting almost all of the aquatic plants, practically speaking, every root possesses a root cap at its tip. It may develop either from the meristematic layer (protoderm) giving rise to the epidermis, or it may be produced by a special meristematic tissue, called the **calyptragen**.

(ii) **The meristematic zone**—This zone lies just behind the root-cap zone. The cells in this region possess denser cytoplasm and larger nuclei than those in other regions, and undergo very active divisions. As a result of this, new cells are being continually added here.

(iii) **The zone of cell enlargement**—This region which lies behind the meristematic zone cannot be clearly differentiated from the latter. Three groups of well-defined meristematic tissues can, however, be noted here ; these are the *protoderm*, the *ground meristem*, and the *procambium*. This zone, along with the preceding one, constitutes the **zone of elongation** or the **growing zone** of the root, which really grows.

(iv) **The zone of maturation**—The cells produced by the meristematic tissues of the zone of enlargement gradually begin

to mature and differentiate out in this region. The central portion of the root, however, remains somewhat undifferentiated in this zone.

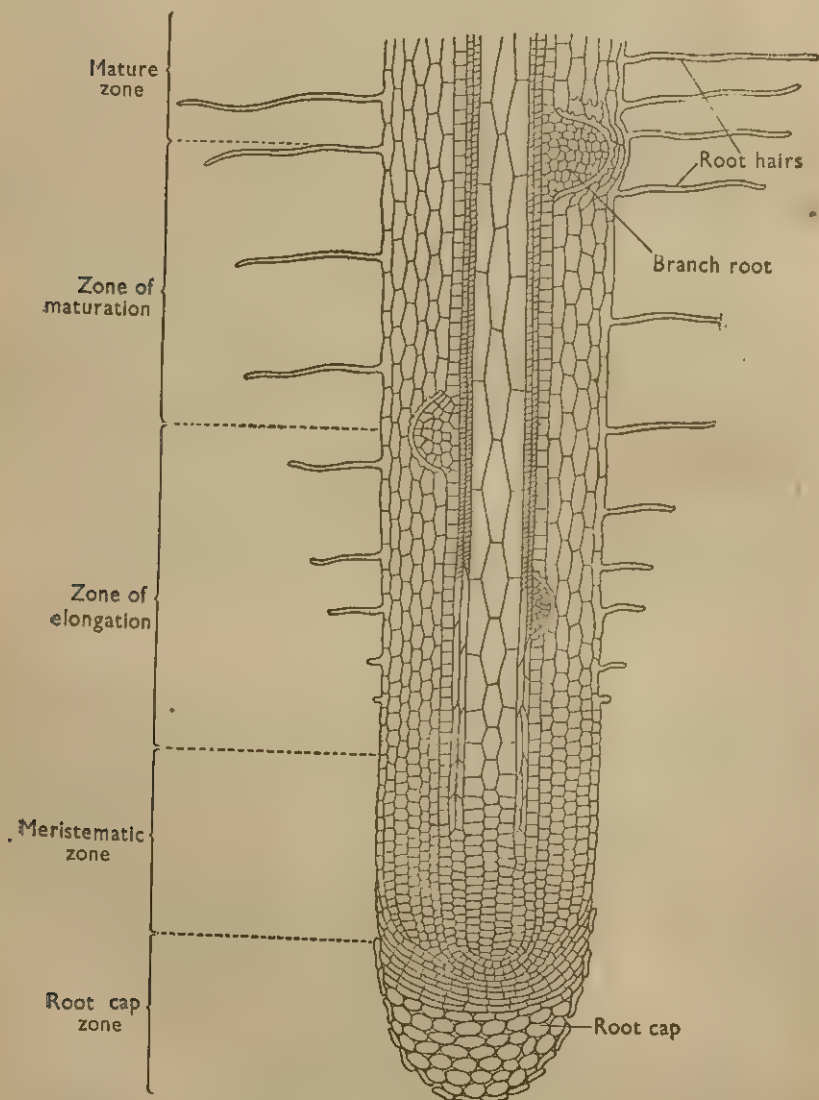


FIG. 20. MEDIAN LONGITUDINAL SECTION THROUGH THE TIP PORTION OF A ROOT SHOWING THE DIFFERENT REGIONS.

(v) **The zone of permanent tissues**—This is also called the **mature zone**. The cells, which began to become mature in the zone of maturation, now attain their permanent shape and size, and give rise to the *primary permanent tissues*. In gymnosperms and dicotyledons mainly, there is a zone of *secondary tissues* beyond this zone of primary permanent tissues, where secondary tissues are produced.*

MODIFIED ROOTS

The roots, whether normal or adventitious, undergo modifications to meet various requirements of plants. The principal types are described below.

MODIFIED TAP-ROOT SYSTEM†

STORAGE ROOTS. Owing to the accumulation of reserve foods, the tap roots become very much swollen and assume different shapes, such as (a) **fusiform**, when it is thickest in the middle and tapers towards both ends, as in English radish‡ (*Raphanus sativus* of Fam. Cruciferae, Fig. 21, A), (b) **conical**, when it is broadest at the base, and gradually tapers towards its apex, as in carrot (*Daucus carota* of Fam. Umbelliferae, Fig. 21, B), and (c) **napiform**, when it is greatly swollen above, but abruptly tapers towards its apical portion, as in turnip (*Brassica campestris* of Fam. Cruciferae, Fig. 21, C), beet (*Beta vulgaris*) of Fam. Chenopodiaceae, *Dahlia variabilis* (Fam. Compositae), bitter cassava or tapioca (*Manihot utilissima*) of Fam. Euphorbiaceae,

*For detailed discussions refer to the internal structures of roots in Part II.

†The familiar examples which are often cited to illustrate the different forms of modified tap roots are, in most cases, really not root alone, but some other parts associated with it, as pointed out by Prof. Priestley as follows :

Radish—hypocotyl and base of leafy stem.

Beet—swollen root and hypocotyl.

Turnip—swollen hypocotyl.

Carrot—swollen root proper.

‡In our country radish, the form of the root is usually conical.

etc. In *Ruellia tuberosa* (Fam. Acanthaceae), the tap root as well as its branches becomes swollen and **tuberous** (Fig. 21, D).

When the primary root as well as its branches are flattened out like discs, they are known as **annulated** or **disciform** roots, as in *ipecac* (*Psychotria ipecacuanha*) of Fam. Rubiaceae (Fig.

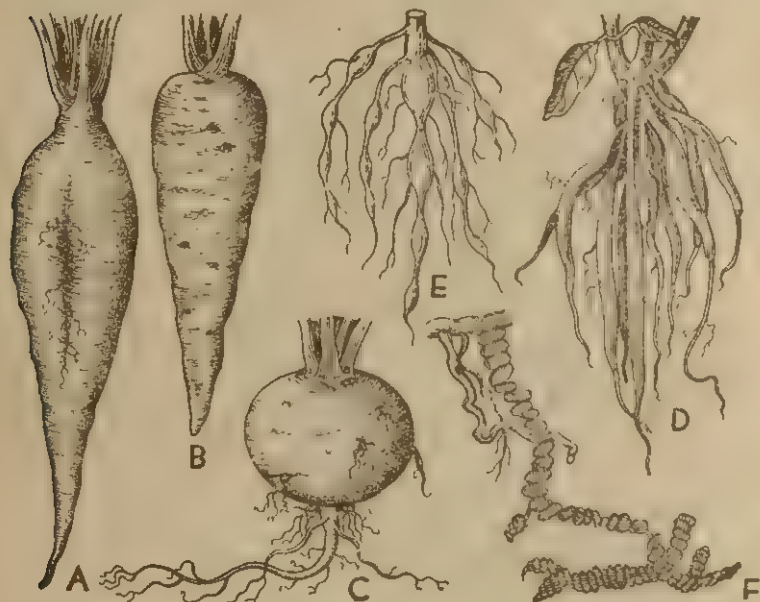


FIG. 21. MODIFIED TAP-ROOT SYSTEM

A, Fusiform ; B, Conical ; C, Napiform ; D, Tuberous ; E, Moniliform ; F, Annulated.

21, F), and when these are alternately swollen and constricted in a beaded manner, they are said to be **moniliform** or **beaded** or **necklace-shaped** roots, as in *Dioscorea daemona* (Fam. Dioscoreaceae, Fig. 21, E), some grasses (Fam. Gramineae) and sedges (Fam. Cyperaceae).

BREATHING ROOTS OR PNEUMATOPHORES*. These are erect roots developed from the normal roots of plants, and grow vertically above the soil or water-level for carrying on respira-

*The pneumatophores are frequently referred to as adventitious roots, but in reality, these are special types of apogeotropic branches of the true roots.

The small, white, inflated, spongy roots of some aquatic plants, like

tion. The apices of those roots are provided with minute pores (pneumathodes), by means of which air is conducted down into the subterranean roots, e.g., *Ceriops roxburghiana* (Fig. 22), *Rhizophora mucronata*, *Bruguiera gymnorhiza*, and other plants of Fam. Rhizophoraceae, *Heritiera*

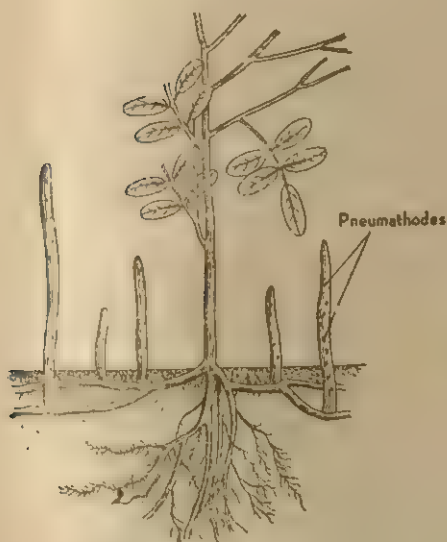


FIG. 22. BREATHING ROOTS OF *Ceriops roxburghiana*.



FIG. 23. BREATHING ROOTS OF *Jussiaea repens*.

minor (Fam. Sterculiaceae), *Sonneratia apetala* (Fam. Sonneratiaceae), *Acanthus illicifolius* (Fam. Acanthaceae), *Aegicerus majus* (Fam. Myrsinaceae), *Aegialitis rotundifolia* (Fam. Plumbaginaceae), *Taxodium distichum*, a gymnosperm, belonging to Fam. Pinaceae, etc.

Sesbania aculeata of S.F. Papilionaceae (Fam. Leguminosae), a very common land plant (mesophyte), also possesses such roots in some cases.

Jussiaea repens (Fam. Onagraceae, Fig. 23), which are produced adventitiously from the nodes of the stems, help in the respiration of the plants. As these roots contain a huge amount of air in them, they also help the plant in floating to some extent.

REPRODUCTIVE ROOTS. Roots usually do not bear any buds, but, in some cases, adventitious buds do arise, and these ultimately give rise to leafy shoots for the purpose of propagation. Such roots are called **reproductive roots**, e.g., palwal (*Trichosanthes dioica*) of Fam. Cucurbitaceae, ipecac (*Psychotria ipecacuanha*) of Fam. Rubiaceae, and other plants, which are very difficult to propagate normally. When injured, sweet potato (*Ipomoea batatas*, Fig. 29, A) of Fam. Convolvulaceae, yam-bean (*Pachyrhizus angulatus* S.F. Papilionaceae of Fam. Leguminosae), *Dahlia* sp. (Fam. Compositae), etc., develop adventitious root buds. Roots, when exposed to light, may produce adventitious buds, which give rise to new plants, as in many fruit trees.

MODIFIED ADVENTITIOUS ROOT SYSTEM

Like normal roots, adventitious roots also undergo modifications as described below.



FIG. 24. ADVENTITIOUS ROOTS
A, Stilt roots ; B, Prop roots.

(a) *Performing special mechanical functions (i.e., fixation support, etc.).*

PROP ROOTS. These roots, arising from the stout horizontal branches of the tree, grow vertically downwards, and on reaching the soil become thick and woody, and thus give support to the branches as pillars, as in banyan [*Ficus benghalensis* (Fig. 24, B)], and India rubber tree (*Ficus elastica*) both of Fam. Moraceae.

STILT ROOTS. These stout roots arise obliquely from the lower part of the trunk, and on reaching the soil help the plant to keep erect, and give additional anchorage to the plant, as found in screwpine (*Pandanus foetidus*) of Fam. Pandanaceae (Fig. 24, A).

ROOT-BUTTRESSES or PLANK-BUTTRESSES. In some huge and heavy trees, plank-like structures, which are partly stems and partly roots, come out in a radiating fashion from the basal region of the trunks. These are known as the **root-buttresses** or **plank-buttresses**, and can be found in plants like silk-cotton tree (*Salmalia malabarica*) of Fam. Bombacaceae, *Sterculia alata* (Fam. Sterculiaceae, Fig. 25), some members of the family Palmae, Moraceae, etc. These buttresses provide stability for the trees.

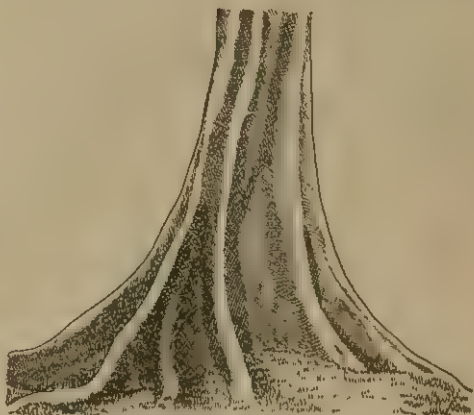


FIG. 25. ROOT-BUTTRESSES

CLIMBING AND CLINGING ROOTS. These roots are found in many weak-stemmed plants, which assist them in climbing up supports. The climbing roots are long clasping roots, which twine round the support, and thus help the plants to climb up, as in *Scindapsus officinalis*, *Pothos aurientum* (Fig. 26)) of Fam. Araceae. The clinging

roots are short ones, which, arising from the stem, enter into cracks and crevices of the supporting tree or wall, or give out a fluid. When this fluid dries up, it makes the stem adherent to the support, and thus helps the plant in climbing, as in betel vine (*Piper betle*) of Fam. Piperaceae, ivy (*Hedera nepalensis*) of Fam. Araliaceae, the epiphytic orchids belonging to Fam. Orchidaceae (Fig. 27), *Podostemon* sp.* (Fam. Podostemaceae), etc.



FIG. 26. CLIMBING ROOTS



FIG. 27. EPIPHYTIC ROOTS

CONTRACTILE or PULL ROOTS (Fig. 28). These roots, which are often found in bulbs and other underground stems, often contract in growth, and pull them deeper into the soil, so that the rosette of leaves is always kept just above the surface of the substratum, as in Indian shot (*Canna indica*) of Fam. Cannaceae, *Crocus sativus* (Fam. Iridaceae), garlic (*Allium sativum*) of Fam. Liliaceae, etc.

ROOT-THORNS. In some palms, the adventitious roots in the lower part of the stem become modified into hard-pointed

*The clinging roots of *Podostemon* are also photosynthetic in nature, and are generally known as holdfasts or haptera.

thorny structures ; these are known as **root-thorns**, as in the American genera *Acanthorhiza* and *Iriartea*.*

(b) *Performing special physiological functions* (i.e., storage, assimilation, etc.).

STORAGE ROOTS. Like normal roots, adventitious roots are also modified for storage purposes. The chief types are : (a) **tuberous**, when some of the adventitious roots become swollen like tubers, as in sweet potato (*Ipomoea batatas*) of Fam. Convolvulaceae (Fig. 29, A), y a m - b e a n (*Pachyrhizus angulatus*) of S.F. Papilionaceae (Fam. Leguminosae), *Orchis maculata* (Fam. Orchidaceae), etc. ; (b) **fasciculated**, when all the fibrous adventitious roots become swollen and seem to arise from a common point at the base of the stem, as in *Asparagus racemosus* (Fam. Liliaceae, Fig. 29, B) ; (c) **nodulose**, when only the apices of adventitious roots suddenly become swollen, as in m a n g o g i n g e r (*Curcuma amada*) and *Costus speciosus* (Fig. 29, C) of Fam. Zingiberaceae.

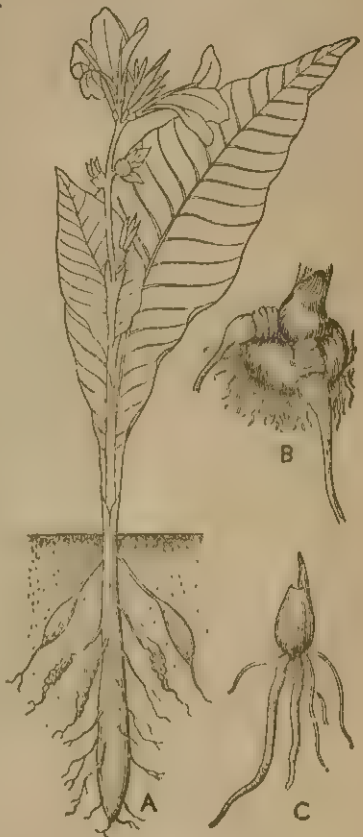


FIG. 28. CONTRACTILE ROOTS
A, of *Canna* ; B, of *Crocus* ; of
Allium.

EPIPHYTIC ROOTS. These are the aerial hanging roots of epiphytes, such as common orchid (*Vanda roxburghii*, Figs. 6, A & 27) of Fam. Orchidaceae. The roots are covered by

*Root-thorns are found in a few other plants also, e.g., *Myrmecodia* sp. (Fam. Rubiaceae), *Bridelia pubescens* (Fam. Euphorbiaceae), *Dioscorea prehensilis* (Fam. Dioscoreaceae), *Moraea* sp. (Fam. Iridaceae), etc.

a thin, greyish structure, known as **velamen**, by means of which moisture is absorbed from the atmosphere.*

PARASITIC ROOTS or HAUSTORIA. These are short, more or less conical roots of parasites, which penetrate into the body of their hosts, and absorb prepared food from them, e.g., dodder (*Cuscuta reflexa*, Fig. 10, A) of Fam. Convolvulaceae, *Orobanche racemosa* (Fam. Orobanchaceae, Fig. 10, D), sandal wood (*Santalum album*) of Fam. Santalaceae, *Balanophora dioica* (Fam. Balanophoraceae, Fig. 11, A), etc.

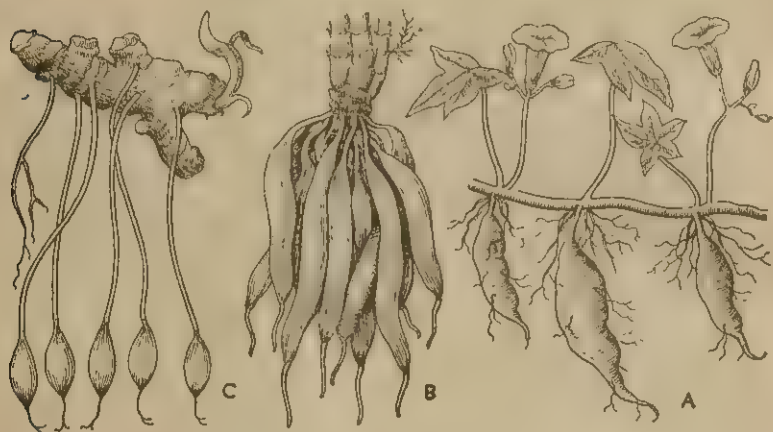


FIG. 29. STORAGE ROOTS

A, Tuberous ; B, Fasciculated ; C, Nodulose.

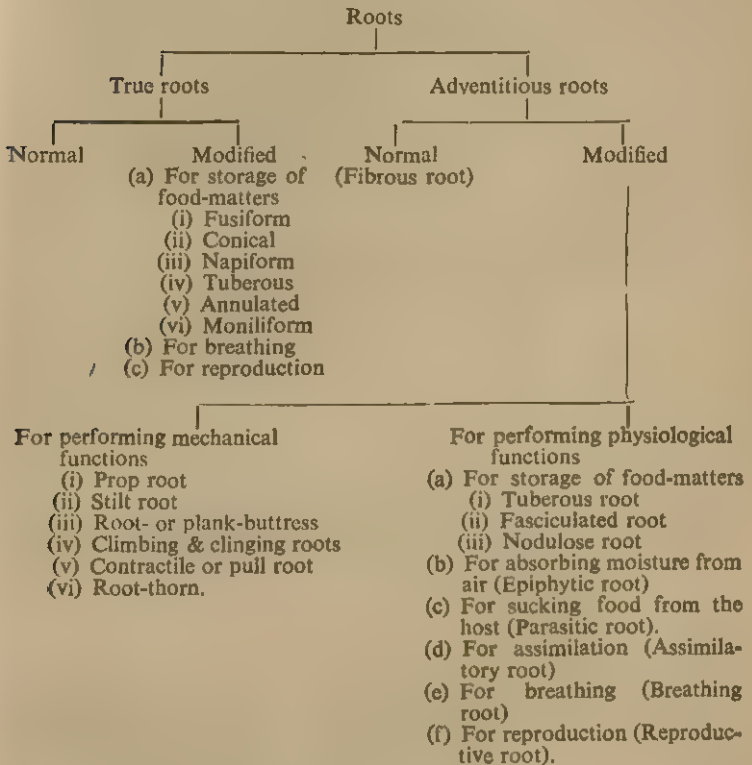
ASSIMILATORY ROOTS. Plants like *Tinospora cordifolia* (Fam. Menispermaceae), *Taeniophyllum* and a few related genera of Fam. Orchidaceae, *Podostemon* sp. (Fam. Podostemaceae), etc., produce long, green, aerial roots, which can prepare carbohydrate foods, with the help of chlorophyll in presence of sunlight from carbon dioxide of the atmosphere and water already absorbed from the soil.

SAPROPHYTIC ROOTS. There are some flowering plants (*Sarcodes* sp. and *Monotropa uniflora* of Fam. Pyrolaceae),

*It should be noted that these aerial roots are green at the tips, and do not grow vertically downwards, whereas the hanging aerial roots of banyan are non-green, and grow vertically downwards.

which grow in soil, rich in humus, and obtain nourishment from it with the help of fungal hyphae, which are found in close association with the root. Such roots are known as **saprophytic roots** and the association is known as **mycorrhiza**.

Roots may be tabulated as follows :



FUNCTIONS OF ROOTS

I. Normal functions. The fundamental functions of the roots are twofold : *mechanical* and *physiological*. The mechanical function is chiefly fixation, *i.e.*, anchoring the plant firmly to the substratum. The physiological functions are : (a) absorption of water containing various nutrient matters in

solution from the soil, (b) conduction (in part) of the absorbed solution in an upward direction, and (c) food storage.

II. **Special functions.** Besides the normal functions, roots also carry on other special mechanical and physiological functions, as stated below :

(a) *Special mechanical functions—*

1. Support to the branches, *e.g.*, Prop roots of banyan.
2. Additional anchorage, *e.g.*, Stilt roots of screwpine.
3. Climbing and clinging, *e.g.*, Climbing roots of *Scindapsus* and clinging roots of betel vine, *etc.*
4. Keeping rosette of leaves at the surface of the soil, *e.g.*, Contractile or pull roots of Indian shot.
5. Protection, *e.g.*, Root-thorns of some palms.

(b) *Special physiological functions—*

1. Storage, *e.g.*, Modified tap roots, and storage roots of sweet potato, *Asparagus*, mango ginger, *etc.*
2. Absorbing moisture from air, *e.g.*, Epiphytic roots of orchids.
3. Absorbing food from host, *e.g.*, Haustoria of dodder.
4. Assimilation, *e.g.*, Assimilatory roots of *Tinospora*.
5. Breathing, *e.g.*, Pneumatophores of *Heritiera* and other mangrove plants; spongy adventitious roots of *Jussiaea*.
6. Reproduction, *e.g.*, Reproductive roots of palwal, yam-bean, *etc.*

ECONOMIC IMPORTANCE OF ROOTS

Many economic products are obtained from the roots of plants. The tuberous roots, like sweet potato, carrot, turnip, beet, *etc.*, form the important sources of human food. In many cultivated crops, as sugar beet, which is a very important source of sugar, the root only is harvested. Some of them provide food for the cattle. Some roots contain high percentages of active chemical substances of great medicinal importance, as in aconite (*Aconitum napellus*) of Fam. Ranunculaceae, gentian (*Gentiana lutea*) of Fam. Gentianaceae, ipecac (*Psychotria ipecacuanha*) of Fam. Rubiaceae, sarsaparilla (*Smilax marcophylla*) of Fam. Liliaceae,

and *Hemidesmus indicus* of Fam. Asclepiadaceae), liquorice (*Glycyrrhiza glabra*) of S.F. Papilionaceae (Fam. Leguminosae), rhubarb (*Rheum officinale*) of Fam. Polygonaceae, etc. Roots of *Ionodium ipecacuanha* (Fam. Violaceae) are sometimes used as true ipecac. From some of them effective insecticides, like pyrethrum powder (obtained from *Chrysanthemum cinerariaefolium* of Fam. Compositae) and rotenone powder are manufactured. Roots of the Russian dandelion (*Taraxacum koksaghyz*) of Fam. Compositae provide a new source of rubber.

CHAPTER II

THE SHOOT

The *stem* along with its *branches* and *leaves* constitute the **shoot system**. It is the direct upward prolongation of the

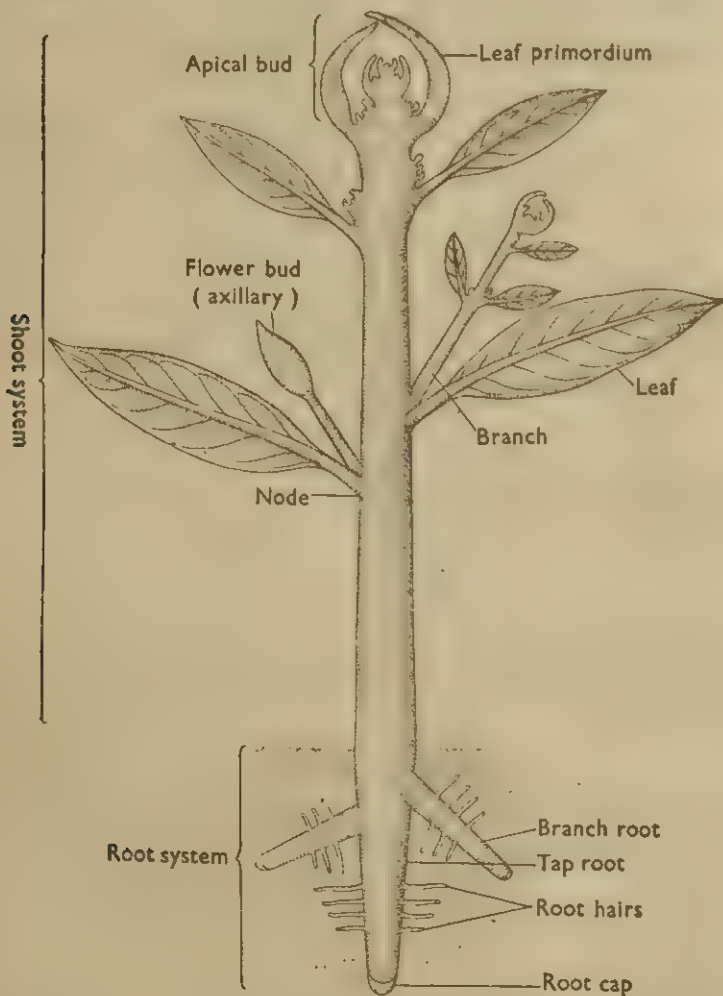


FIG. 30. SEMI-DIAGRAMMATIC REPRESENTATION OF THE DIFFERENT ORGANS OF AN ADULT PLANT.

plumule. A plant normally has three developmental phases : the *embryonic*, the *seedling*, and the *adult*. In the embryonic stage, its body consists of the plumule, which may be regarded as the embryonic shoot, the cotyledons as the embryonic leaves and the radicle as the embryonic root. In the seedling stage, it consists of the primary root with one or two branches, the long or short hypocotyl, the cotyledons (which, in some cases, form the first pair of green foliage leaves), the young stem with a few normal leaves (*i.e.*, the developing shoot) and the terminal and axillary buds. In the third or the adult stage, the stem continues its development as the main axis, giving rise to new leaves as it grows upward. In the axils* of these leaves new *buds* arise, later on developing into lateral branches, which in their turn bear leaves and buds (both terminal and axillary). The tap root gives rise to laterally developed branch roots, and thus establishes the root system. In this way, the adult plant enlarges, and assumes its definite size and shape (Fig. 30).

THE BUD

A *bud* (Fig. 31) is an embryonic shoot in a dormant condition. It is essentially a conical mass of meristematic tissue, while in

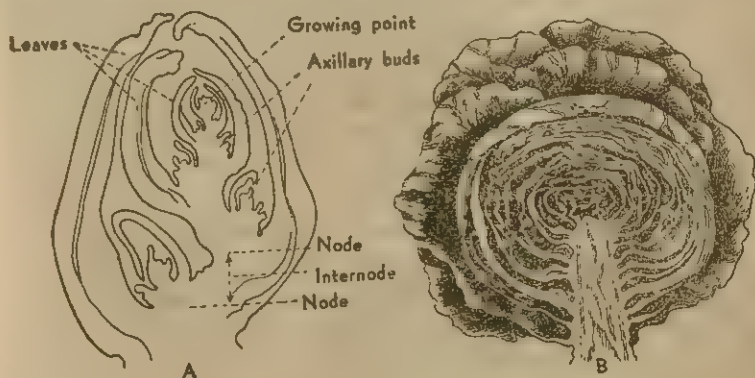


FIG. 31. THE BUDS

A, Longitudinal section of a bud ; B, the same of cabbage.

some cases, it consists of rudimentary short nodes, each bearing one or more young leaves, compressed internodes and, a growing

*The angle formed between the leaf stalk and the stem is called the *axil*.

point (Figs. 31, A & 37). These crowd together, and overlap the apex, as in the cabbage (*Brassica oleracea*, Fig. 31, B) of Fam. Cruciferae, which is regarded as the largest of all buds. It is by gradual unfolding of the leaves and the elongation of the successive internodes that the growth of the axis takes place, and the leaves are separated and ultimately expanded from the rudimentary state. It should be noted in this connection, that the *plumule is the first bud*, and this bud-configuration is maintained at the tip of the gradually elongating axis throughout the life of the individual.

KINDS OF BUDS

Buds, differing in their nature, are found at different positions on the plant, and may be broadly classified into four groups. Thus, there may be **leaf bud**, developing into a leafy shoot ; **stem bud** (or **branch bud**), growing out into a new leafy twig ; **flower bud**, giving rise to a flower ; and **mixed bud**, giving rise to both the vegetative shoot and the flower, as in apple (*Pyrus malus*) of Fam. Rosaceae, lilac (*Syringa vulgaris*) of Fam. Oleaceae, buckeye (*Aesculus ohioensis*) of Fam. Hippocastanaceae, etc.

Usually, buds are found singly at the apex of the elongating axis, or in the axils of leaves, and are called **normal buds**. But, buds do arise laterally from positions other than the normal ones, and are then known as **adventitious buds**. The normal buds may be arranged either in an *alternate* or *spiral* fashion, that is, only one bud develops at each node, as is found in the majority of the plants, or they may be *oppositely* arranged, when two buds are formed at each node on opposite sides of the stem or its branches, as can be seen in maple (*Acer campestre*) of Fam. Aceraceae. In some rare cases, in some members of the families Bignoniaceae and Rubiaceae, more than two buds are developed in a *whorled* manner at each node.

Normal buds, when situated at the apex of the axis, are called **terminal** or **apical buds** (Fig. 32, A). Buds arising in the axils of leaves are called **axillary** or **lateral buds** (Fig. 32, A). In herbaceous plants, these buds are either very small or buried completely in the tissue of the stem, so that their presence is entirely obscure. Axillary buds may be *alternate*, *opposite* or *whorled*, giving rise

to the respective mode of branching. The increase in length of plant takes place by the growth of the terminal bud, while the branch system is primarily dependent on the activity of the axillary buds. But, all the axillary buds do not develop into leafy shoots ; only a few may be **active**, while the majority of these remain **dormant**. In some perennial woody stems, these dormant buds may grow out into branches under suitable conditions of stimulus. For example, if the main shoot is cut off, the dormant axillary buds develop into vigorously growing branches. Sometimes, buds, instead of developing into shoots, fall off, and are known as **deciduous buds**.

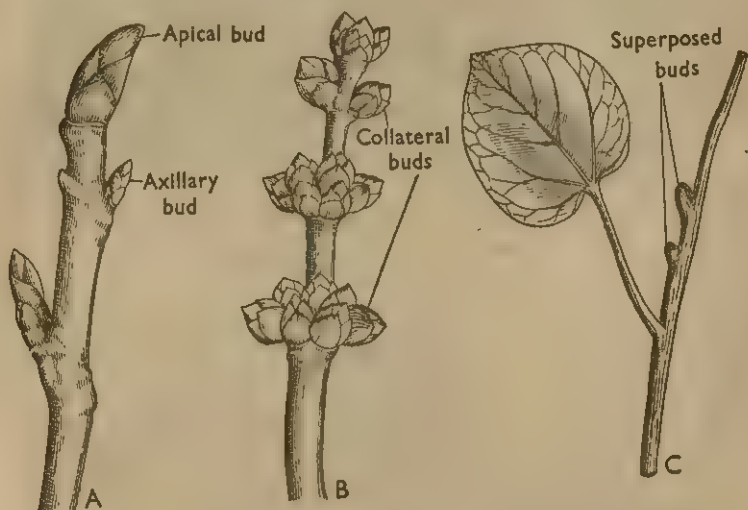


FIG. 32. DIFFERENT TYPES OF BUD

A, Apical and axillary buds in *Aesculus* ; B, Collateral buds in *Acer* ;
C, Superposed buds in *Aristolochia*.

Occasionally, along with a normal bud, there arise two or more buds, usually in a group of three, in or near the same axil. According to their position, with respect to one another, these may be either **collateral**, i.e., placed side by side, as in brinjal (*Solanum melongena*) and chilli (*Capsicum annuum*) of Fam. Solanaceae, gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, sugar maple (*Acer saccharum* of Fam. Aceraceae, Fig. 32, B), or **superposed**, i.e., placed one above the other, as in *Aristolochia*.

altissima (Fam. Aristolochiaceae, Fig. 32, C), walnut (*Juglans regia*) of Fam. Juglandaceae, etc. Such buds, excepting the normal ones, are called **accessory** or **supernumerary buds**. Sometimes, superposed buds are seen to arise on the stem, a little above the axil, when these are known as **extra-axillary buds**.

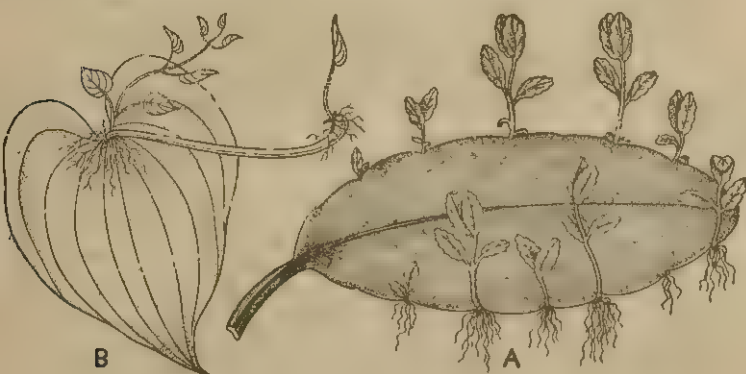


FIG. 33. EPIPHYLLOUS BUDS
A, of *Bryophyllum*; B, of *Begonia*.

The form of a plant is dependent, to a large extent, upon the number and position of its buds, as well as upon the time and mode of their development. If the terminal bud is very active and the axillary ones dormant, then the plant grows in length. On the other hand, if the axillary buds are much more active in comparison to the rather slow-growing terminal one, the plant assumes a bushy habit.

Adventitious buds may be **epiphyllous**, i.e., arising on leaves, as in *Begonia* sp. (Fam. Begoniaceae, Fig. 33, B), *Bryophyllum calycinum* (Fig. 33, A), and *Kalanchoe spathulata* of Fam. Crassulaceae, etc. At the proper season when plants are pruned or pollarded, many adventitious buds develop on stems, eventually producing new shoots, as in *Duranta plumieri* (Fam. Verbenaceae); such buds are termed as **cauline**. In some cases, they are said to be **radical**, when they arise on roots, as in *Calwal* (*Trichosanthes dioica*) of Fam. Cucurbitaceae, coffee (*Coffea arabica*) and ipecac (*Psychotria ipecacuanha*) of Fam. Rubiaceae, etc.

Sometimes, flower buds, appearing normally in the axils of leaves, get shifted from their original positions in course of development, and appear to have arisen either from the stem, or from the bract, or from the mid-region of the lamina as are



FIG. 34. ADNATED BUDS
A, in *Cuphea* ; B, in *Tilia* ; C, in *Helwingia*.

found in *Cuphea micropetala* of Fam. Lythraceae (Fig. 34, A). *Tilia ulmifolia* of Fam. Tiliaceae (Fig. 34, B), and *Helwingia* sp. of Fam. Cornaceae (Fig. 34, C), respectively. Such buds are known as **adnated buds**.

MODIFIED BUDS

Buds normally help in the elongation of the plant, as well as giving it a definite shape and protecting its delicate, growing stem tip. But sometimes, as occasions arise, they become modified to carry on special functions as follows.

Self-defence. Sometimes, the axillary buds become modified into hard, pointed, and thorny structures, as in *Duranta plumieri* (Fam. Verbenaceae), and glory of the garden (*Bougainvillea spectabilis*) of Fam. Nyctaginaceae.

Climbing. In some cases, the terminal buds are modified into apparently lateral tendrils, as in *Vitis quadrangularis* and *V. pedata* of Fam. Vitaceae.

Propagation. The best example is our common *Globba bulbifera* of Fam. Zingiberaceae (Fig. 35, B), where buds lying in the axils of bracts become swollen and globular in form due to accumulation of food matters, and thus become metaporphozed in structure. Such modified buds are called **bulbils**, which,



FIG. 35. BULBILS

A, of *Dioscorea bulbifera* ; B, of *Globba bulbifera*.

when mature, detach themselves from the parent plant, fall on the ground and produce new plants. In the case of *Dioscorea bulbifera* (Fam. Dioscoreaceae, Fig. 35, A) the bulbils arise in the axils of foliage leaves. A large number of floral buds in *Agave americana* and *Fourcroya longaeva* of Fam. Amaryllidaceae become modified into bulbils, which are capable of germinating while still attached to the inflorescence.

PROTECTION OF BUDS

Buds sometimes require protection, as they are often exposed to extremes of temperature, and there are various adaptations to cope with such situations. Thus, buds may be protected by means of : (a) scale leaves, as in *Michelia champaca* (Fam. Magnoliaceae), jack (*Artocarpus heterophylla*-*A. integrifolia*, Fig. 36, A)

and banyan (*Ficus benghalensis*) of Fam. Moraceae ; (b) leaf base acting as a sheath as in *Wormia burbizioides* (Fam. Dilleniaceae, Fig. 36, B) ; (c) a coating of dense hairs, as in jujube (*Zizyphus*



FIG. 36. PROTECTION OF BUDS

A, by scale ; B, by sheathing leaf base ; C, protected buds of *Acer*.

jujuba) of Fam. Rhamnaceae ; (d) a coating of wax, oil or resinous or mucilagenous matter to prevent loss of water from their surface, as in *Aesculus indicus* (Fam. Hippocastanaceae) ; and (e) their deeply seated position in the bark, as in camphor (*Camphorum aromaticum*) of Fam. Lauraceae. Buds, when protected by scales, are called **covered** or **protected buds** (Fig. 36), and when not provided with any such protective structure, **naked buds** ; the latter ones are characteristics of all herbaceous and woody plants of moist tropics.

THE STEM

The first stem originates from the epicotyl of the embryo axis of the seed, and forms the ascending axis of the shoot. This may remain simple and unbranched throughout the life of the plant, as in palms, or, may give out lateral branches in course of its growth. These, in their turn, give out similar lateral members, and in this way, the plant assumes a definite form. The stem is normally erect and subaerial, but occasionally it may subterranean

or may creep along the surface of the soil, or climb upon support ; in still others, it may be so much condensed and insignificant, that the plant appears to be stemless (*acaulescent*), as in radish (*Raphanus sativus*) of Fam. Cruciferae, onion (*Allium cepa*) of Fam. Liliaceae, etc.

DIFFERENT REGIONS OF A STEM (Fig. 37)

As in the case of a root, the growing stem tip can be differentiated into four regions, which are also found to be merging almost imperceptibly one into another. From the extreme tip

proceeding downwards, these regions can be called : the *formative* or the *meristematic region*, the *region of elongation*, the *region of maturation*, and the *permanent* or *mature region*.

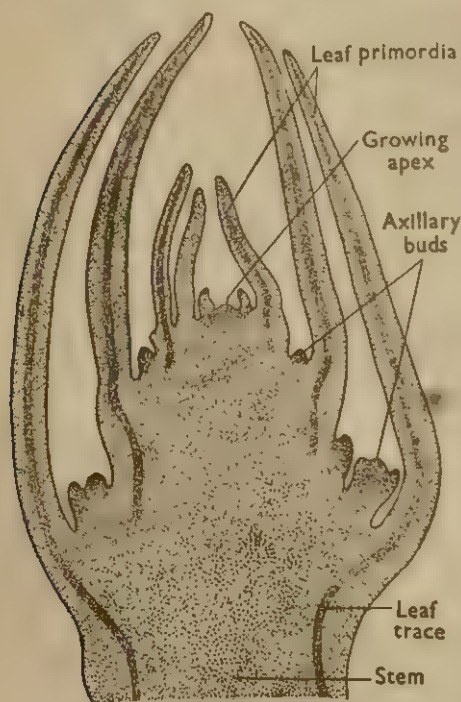


FIG. 37. MEDIAN LONGITUDINAL SECTION THROUGH THE APICAL PORTION OF A STEM SHOWING THE DIFFERENT PARTS.

(i) The *formative* or *meristematic region*—This region occurs at the extreme apex of the stem, and here the cells are in an active state of division. Along the sides of the meristematic region outgrowths, referred to as *leaf primordia*, appear, which later on develop into mature leaves, usually bearing axillary buds.

(ii) The *region of elongation*—This region lies next below the formative region. Here the cells usually stop dividing, and begin to enlarge in size. Rapid elongation, in the case of a vigorously growing stem, gene-

really commences in the third or the fourth internode from the apex of the stem.

(iii) **The region of maturation**—In this region, where cell division is already brought to a close, the various types of cells begin to differentiate out into respective tissues.

(iv) **The mature region**—This region is characterized by having the cells becoming completely differentiated (both structurally as well as functionally) into various tissues. These tissues are known as *permanent tissues*, and they may be *primary* or *secondary*.

CHARACTERISTIC FEATURES

The stem has certain characteristic features. By these, even the underground stems, which are often mistaken for roots, may be distinguished from the latter. The stem or its branches bear leaves, leaf buds, flowers, and flower buds. They normally grow towards the source of light, and may be green while young. The branches are sub-epidermal in origin. The apex of the stem is never protected by a cap, but is usually terminated by a bud. The differentiation of the stem into nodes and internodes is another characteristic feature. Multicellular hairs may be present on the surface of the stem.

FORMS OF STEM

The form of the stem varies in different plants. It is usually **cylindrical**, which, when cut transversely, shows a more or less circular outline. Occasionally, however, it may be **angular** : three-angled in sedge (*Cyperus rotundus*) and other plants of Fam. Cyperaceae, four-angled in basil (*Ocimum sanctum*) and other plants of Fam. Labiatae, *Peristrophe bicalyculata* (Fam. Acanthaceae), *Lantana camara* (Fam. Verbenaceae), *Vitis quadrangularis* (Fam. Vitaceae), etc. ; **flattened**, as in *Coccoloba platyclados* (Fam. Polygonaceae), prickly pear (*Opuntia dillenii*) of Fam. Cactaceae, etc. ; **fistular** or **hollow**, as in grasses, bamboo (*Bambusa arundinacea*) of Fam. Gramineae ; **articulated** or **jointed**, as in sugarcane (*Saccharum officinarum*) of Fam. Gramineae ; or **ribbed**, i.e., showing alternate ridges and furrows, as in gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, and *Equisetum* sp. (Fam. Equisetaceae), a pteridophyte.

SURFACE OF STEM

The surface of stem may be **glabrous**, *i.e.*, perfectly smooth, as in China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, periwinkle (*Vinca rosea*) of Fam. Apocynaceae, *Fimbristylis campanulata* (Fam. Cyperaceae), *etc.*; **glaucous**, *i.e.*, when smooth and somewhat shining with a bluish tinge, as in *Solanum glaucum* (Fam. Solanaceae); **hispid** or **hairy**, *i.e.*, covered with hairs, as in *Clerodendron infortunatum* and *Lantana camara* of Fam. Verbenaceae, *Ocimum sanctum* (Fam. Labiatae), *Fleurya interrupta* (Fam. Urticaceae), *Chrozophora plicata* and *Tragia involucrata* of Fam. Euphorbiaceae, *etc.*; **prickly** or **spiny**, *i.e.*, provided with prickles or spines, as in rose (*Rosa centifolia*) of Fam. Rosaceae, *Solanum ferox* (Fam. Solanaceae), *etc.*

KINDS OF STEM

The aerial stems may be divided into several categories. According to their nature and size, they may be herbaceous or woody, and depending on the nature of their habit, they may be erect or weak.

Herbaceous stems or **herbs** are small-sized plants with soft stems. According to the duration of life, herbs may be annuals, biennials and perennials. Those herbs, which live and complete their life-cycles in one season only, are called **annuals**, such as pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae), mustard (*Brassica nigra*) of Fam. Cruciferae, paddy (*Oryza sativa*) of Fam. Gramineae, *etc.* **Biennials** complete their life-cycles in two successive seasons. True biennials are rare in our country. Some plants, such as radish (*Raphanus sativus*) of Fam. Cruciferae, carrot (*Daucus carota*) of Fam. Umbelliferae, *etc.*, are, however, regarded as examples of biennials. In the first season, the biennials store up food materials within them, mainly in their roots, and these are utilized in the next season for the production of flowers and fruits. Plants which live for more than two seasons are called **perennials**, such as ginger (*Zingiber officinale*), turmeric (*Curcuma longa*), Indian shot (*Canna indica*), banana (*Musa paradisiaca* var. *sapientum*), and other plants belonging to the Order Scitamineae. The perennial herbs send out aerial shoots for vegetative and reproductive purposes once a year during the periods favourable for growth. With the advent of unfavourable period, *i.e.*, winter, the aerial shoots die down to the

ground, and the plants survive the period through the underground stems.

Woody-stemmed plants may be either shrubs or trees, depending on the nature of the main stem and its branches. **Shrubs** are small, perennial, woody plants without a clearly differentiable main trunk, as in China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, *Abroma augusta* (Fam. Sterculiaceae), custard apple (*Anona squamosa*) of Fam. Anonaceae, rose (*Rosa centifolia*) of Fam. Rosaceae, Mexican jasmine (*Cestrum nocturnum*) of Fam. Solanaceae, etc. The main axis branches very early near the ground. Each branch develops as vigorously as the mother axis, so that, ultimately it becomes difficult to distinguish the main stem from its branches. **Trees** are taller and more robust than the shrubs. Their main axis remains unbranched for some distance above the ground, and forms the **trunk**. These are also perennial plants. Familiar examples are mango (*Mangifera indica*) of Fam. Anacardiaceae, tamarind (*Tamarindus indica*) of S.F. Caesalpinieae (Fam. Leguminosae), banyan (*Ficus benghalensis*) of Fam. Moraceae, mast tree (*Polyalthia longifolia*) of Fam. Anonaceae, etc. In spite of the technical differences between the shrubs and the trees, sometimes, however, it is difficult to distinguish the former from the small-sized trees.

Erect stems are typically more or less cylindrical in shape, branched or unbranched, and are strong enough to maintain an upright position. There are some monocotyledonous plants, such as, coconut palm (*Cocos nucifera*), palmyra palm (*Borassus*



FIG. 38. CAUDEK

flabellifer) and others of Fam. Palmae, in which the main stem is very tall, erect, unbranched, with semi-circular scars, and bearing a crown of leaves at its summit. Such an erect stem is known as a **caudex** (Fig. 38). The terms **culms** or **haulms** are given to the erect and close-jointed stems of sugarcane (*Saccharum officinarum*) and bamboo (*Bambusa arundinacea*) of Fam. Gramineae.

Weak-stemmed plants are those, whose stems are not rigid enough to maintain an upright position, hence, they either trail along the surface of the soil, or climb up supports. The former kinds of plants are called **trailers**, and the latter, **climbers**.

The **trailing plants** or **trailers** (Fig. 39) are of the following three kinds :—

Decumbent. When the stems lie on the ground without rooting at the nodes, and with apices of the branches as well as those of the main stems turned upwards, as in *Lindenbergia urticaefolia* (Fam. Scrophulariaceae, Fig. 39, A). *Tridax procumbens* (Fam. Compositae), *Lobelia irigona* (Fam. Campanulaceae), *Basella rubra* (Fam. Basellaceae), etc.

Procumbent. When the stems are as in the decumbent ones, but their apices lie flat on the ground, as in toad flax (*Linaria ramosissima*, Fig. 39, B) of Fam. Scrophulariaceae.

Creeping. When the stems not only lie flat on the ground



FIG. 39. TRAILERS
A, Decumbent ; B, Procumbent ; C, Creeping.

but also root at the nodes, as in *Cynodon dactylon* (Fam. Gramineae), *Lippia nodiflora* (Fam. Verbenaceae, Fig. 39, C), *Evolvulus nummularius* (Fam. Convolvulaceae), etc.

The **climbers** climb up other plants or neighbouring objects

by their stems or by means of special devices. They are of the following types.

Stem climbers or twiners. These plants climb up by twining their stems around the objects. According to the direction of twining, twiners may be **dextrorse**, *i.e.*, when the twining is from the left to the right or clockwise, as in *Mikania scandens* (Fam. Compositae), *Dioscorea alata* (Fam. Dioscoreaceae), *etc.*, or **sinistrorse**, *i.e.*, when the twining is from the right to the left or anti-clockwise, as in *Clitoria ternatea* of S.F. Papilionaceae (Fam. Leguminosae), *Ipomoea quamoclit* (Fam. Convolvulaceae), *etc.* Twiners like *Hiptage madablota* (Fam. Malpighiaceae), *Aganosma caryophyllata*, *Ichnocarpus fruticosa*, *Beaumontia grandiflora* of Fam. Apocynaceae, *Dragea volubilis* (Fam. Asclepiadaceae), some species of *Bauhinia* of S.F. Caesalpinieae (Fam. Leguminosae), *etc.*, have long and woody stems, which climb up big trees ; such woody stem climbers are called **lianes**. Some of these bauhinias, growing in tropical rain-forests, often extend from one tree to the other, forming loops and wreaths.

Root climbers. These plants climb by means of special adventitious roots, which develop along the sides of the stem in contact with the support, often forming an intricate network of roots, which act as holdfasts, as in *Scindapsus officinalis* and *Pothos auriens* of Fam. Araceae, betel vine (*Piper betle*) of Fam. Piperaceae, ivy (*Hedera nepalensis*) of Fam. Araliaceae, *etc.*

Tendrill climbers. These plants climb by means of thread-like structures, called **tendrils**, which are very sensitive to contact. These tendrils, by coiling round the support, help the plant in climbing, and are either modified stems, as in passion flower (*Passiflora suberosa*) of Fam. Passifloraceae, *Vitis quadrangularis*, grape vine (*V. vinifera*) of Fam. Vitaceae, *etc.*, or leaves, as in wild pea (*Lathyrus aphaca*) of S.F. Papilionaceae (Fam. Leguminosae), or leaflets, as in *Naravelia zeylanica* (Fam. Ranunculaceae), pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae), or leaf apex, as in glory lily (*Gloriosa superba*) of Fam. Liliaceae, *etc.* In some cases, the inflorescence axis (*Quisqualis malabaricum* of Fam. Combretaceae), and the lateral flowers of a dichasium (*Cardiospermum halicacabum* of Fam. Sapindaceae) also act as the tendril.

Petiole climbers. These plants climb by twisting their petioles round the support, as found in virgin's bower (*Clematis gouriana*) of Fam. Ranunculaceae, *Aristolochia indica* (Fam. Aristolochiaceae), garden nasturtium (*Tropaeolum majus*) of Fam. Tropaeolaceae, etc.

Hook climbers. These plants climb by means of curved hooks developed from the flower-stalks, as in *Artabotrys odoratissima* (Fam. Anonaceae). The hooks clasp the support, and in



FIG. 40. CLIMBERS
A, Rambler ; B, Hook climber.

some species of *Artabotrys* as well as in *Uncaria pilosa* (Fam. Rubiaceae), these structures, after catching hold of the support, enlarge and ultimately become hard and woody. In *Bignonia anguis-cati* (Fam. Bignoniaceae), these hooks are the modified terminal leaflets (Fig. 40, B), which assist the plant in climbing its support.

Ramblers or scramblers. These plants simply rest, scramble and stick to other plants or supports with the help of prickles and spines, as in glory of garden (*Bougainvillea spectabilis*) of Fam. Nyctaginaceae, cane palm or rattan (*Calamus*

rotang)* of Fam. Palmae, fever nut (*Caesalpinia bonducella*) of S.F. Caesalpinieae (Fam. Leguminosae), *Capparis zeylanica* and *C. sepiaria* of Fam. Capparidaceae, *Pisonia aculeata* (Fam. Nyctaginaceae), and certain roses.

MODIFIED STEMS

The modified stems are of two kinds : (a) **subaerial**, and (b) **subterranean or underground**.

A. *Subaerial modified stems* (Fig. 41) :

The subaerial modified stems are chiefly meant for vegetative propagation. They are of the following kinds.

Runner. It is a slender, prostrate branch, which arises from the axil of a leaf close to the ground, runs along the surface of the soil for some distance and produces new roots and leaves at its tip. In this manner, a single plant spreads over a large area in course of a very short time. All these daughter branches remain connected at first to the parent plant, but later on form separate individuals. Common examples are wood sorrel (*Oxalis corniculata*, Fig. 41, A) of Fam. Oxalidaceae, *Ipomoea reptans* (Fam. Convolvulaceae), Indian pennywort (*Hydrocotyle asiatica*) of Fam. Umbelliferae, *Marsilea* (a pteridophyte), etc.

Stolon. Like runner, it is also a slender branch but is somewhat longer. Owing to its great length, the branch arches or bends downwards instead of running horizontally over the surface of the ground. Its tip, on reaching the soil, produces roots as well as a leafy shoot, as in peppermint (*Mentha piperita*, Fig. 41, B) of Fam. Labiatae, wild strawberry (*Fragaria nilgherensis*) and a few other plants of Fam. Rosaceae, etc.

Offset. It is also a prostrate branch, but is shorter and thicker than the runner. The tip ends in a tuft of roots and a rosette of leaves. Common examples are water hyacinth (*Eichhornia*

*In the rattans (Fig. 40, A), both the stems as well as leaves are provided with many recurved spiny structures, which help the plants in scrambling over their supports. In addition to these, the rachis of the leaves also end in barbed whip-like structures, called *flagella*, which twine round the supports and thus help in climbing.

crassipes) of Fam. Pontederiaceae, water lettuce (*Pistia stratiotes*, Fig. 41, C) of Fam. Araceae, etc.



FIG. 41. SUBAERIAL MODIFIED STEMS
A, Runner ; B, Stolon ; C, Offset ; D, Sucker.

Sucker. It is also a branch, but it originates from the underground portion of the stem of the parent plant. It proceeds horizontally under the surface of the soil for a short distance before emerging into the air, and eventually produces a leafy aerial shoot and adventitious roots. *Chrysanthemum coronarium* (Fam. Compositae, Fig. 41, D), mint (*Mentha viridis*) of Fam. Labiatae, etc., are common examples.

It is to be noted that both sucker and stolon have erect shoots.

B. Subterranean modified stems (Fig. 42) :

The plants are, in some cases, perennials and perennate through unfavourable conditions with the help of these modified underground stems. They produce leaves and flowers during

the vegetative season, manufacture food and store them in the underground stems. With the advent of winter, the aerial parts die down, and the plants manage to survive the period through these underground stems in a more or less resting condition. Thus, primarily these stems are organs of perennation and storage, but secondarily they are also means of vegetative propagation. The underground modified stems are of the following types.

Rhizome. It is a thick, elongated, dorsoventral stem or branch, which becomes thick owing to deposition of food matters in its body. It grows horizontally under the surface of the soil or remains partly buried under it. It is characterized by the pre-

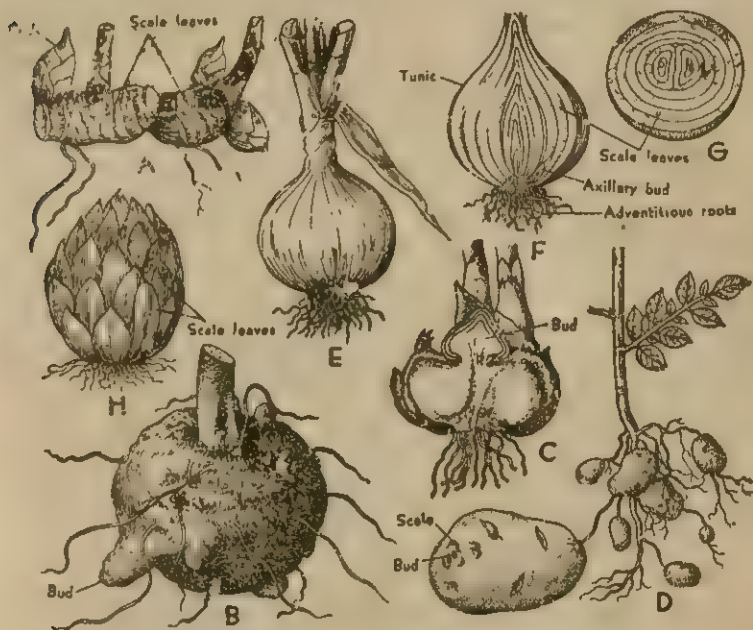


FIG. 42. SUBTERRANEAN MODIFIED STEMS

A, Rhizome ; B, Corm ; C, the same of *Crocus* in l.s. ; D, Tuber ;
E, Tunicated bulb ; F, the same in l.s. ; G, the same in t.s. ;
H, Scaly bulb.

sence of distinct nodes and internodes, and at each node there is a brownish scale leaf having a bud in its axil. From some of these axillary buds aerial shoots are produced annually bearing

foliage leaves and flowers. Large number of adventitious roots are given off mainly from its lower surface. The rhizome usually branches freely. At the growing region there is a terminal bud, which either develops into a new aerial shoot or helps in the elongation of the rhizome, while the older parts die down behind. When the aerial shoots die, they leave scars in the form of rings on the upper surface of the rhizome. Familiar examples are ginger (*Zingiber officinale*), turmeric (*Curcuma longa*), Indian shot (*Canna indica*, Fig. 42, A), banana (*Musa paradisiaca* var. *spientum*) and other plants belonging to the Order Scitamineae.

In some cases, as in *Alocasia indica* (Fam. Araceae), water-lily (*Nymphaea stellata*) and lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae, etc., the rhizome grows more or less vertically. A stout and vertical rhizome is known as **root-stock**. A slender, horizontal rhizome with long internodes is called a **sobole**, as in seashore grass (*Spinifex squarrosus*) and *Cynodon dactylon* of Fam. Gramineae.

Stem-tuber or tuber. It is a swollen underground branch or part of a branch, arising in the axil of a leaf on the main stem. It is round, or oval in shape, with one or several condensed internodes, and is provided with the so-called 'eyes'. Each eye is situated in a depression and consists of a bud in the axil of a minute scale leaf. Roots usually do not develop from the tubers, but, when placed under favourable conditions, axillary buds grow out to produce new shoots, from the bases of which adventitious roots are developed. Common examples are potato (*Solanum tuberosum*, Fig. 42, D) of Fam. Solanaceae, sedge (*Cyperus rotundus*) and *Scirpus grossus* of Fam. Cyperaceae, artichoke* (*Helianthus tuberosum*) of Fam. Compositae, etc.

Corm or solid bulb. This type of underground stem is more or less rounded, stout, solid, trunk-like in form and grows vertically. Buds are produced at the nodes in the axils of thin and membraneous scale leaves, which are minute and scattered all over its body. Some of the buds may grow out and swell to form new young corms; the old corm shrivels up and eventually dies. Adventitious roots develop either from all over its body or from its base. The terminal bud is relatively large, which,

*It illustrates both rhizome and tuber; tubers are edible.

during early spring, grows out to form large foliage leaves and flowers. Common examples are teliga potato* (*Amorphophallus campanulatus*, Fig. 42, B) and common arum† (*Colocasia anti-quorum*) of Fam. Araceae, saffron (*Crocus sativus*, Fig. 42, C) and meadow saffron (*Colchicum autumnale*) of Fam. Liliaceae, etc.

Bulb. The term is applied to a modified underground bud-like structure. The axis, i.e., the stem, is extremely reduced to a short, broad and convex **disc** with compressed internodes. From its upper surface leaves develop completely covering the stem with their thick, fleshy and concentrically arranged leaf-bases; the aerial green portions, however, usually die down. In the axils of these leaves there arise axillary buds, some of which may enlarge to form new young bulbs. Adventitious roots are given off from the lower surface of the stem. At the centre of the disc there is a terminal bud, which produces aerial leaves or a scape.

Bulb is of two kinds :

(a) **Tunicated** or **coated**, when the fleshy leaf-bases are regularly arranged and enclose one another in a concentric manner, the outer ones being dry and membranous to form the *tunic* or coat, as in onion (*Allium cepa*, Figs. 42, E-G) of Fam. Liliaceae.

(b) **Scaly** or **naked**, when numerous thick and fleshy leaves simply overlap one another and are not covered with a tunic, as in tulip (*Tulipa gesneriana*) and white lily‡ (*Lilium candidum*, Fig. 42, H) of Fam. Liliaceae. In these cases, the food-storing organs are not the stems but the fleshy underground leaf-bases.

**Amorphophallus campanulatus*, which is often cited as a familiar example of corm, in reality consists of one swollen internode only, situated at the base of a conical terminal bud. It does not bear any scale leaf on its surface, but numerous adventitious roots may develop from it. A few adventitious buds in the form of daughter corms may also arise from its side. Annual much-branched leaves are produced from its upper side. The old corm gradually shrivels up and is replaced by the formation of another corm developed from the next upper internode of the apical bud.

It should also be noted that the so-called much-branched leaf really consists of three leaves united by the petioles to form a common stalk (=so-called petiole).

†It illustrates both corm and runner.

‡In white lily the leaf-bases are sometimes reduced to scales.

It is to be noted that garlic (*Allium sativum*) of Fam. Liliaceae illustrates both the tunicated and scaly bulb.

METAMORPHOSED STEMS

In the cases mentioned above, the stem nature of the modified organ is not entirely changed. But there are cases, where the stem is modified to such an extent, that it becomes extremely difficult to find out its real morphological nature. In such cases, therefore, we have to look for their origin and internal structure before assigning them any morphological value. Such instances of extreme modifications are designated by the term **metamorphosis**, and the stems are said to be **metamorphosed**. A brief account of the metamorphosed stems is given below.

Thorn or stem-spine (Fig. 43). Sometimes, the axillary branches may become arrested in their growth and are metamorphosed into hard, sharp-pointed structures, called **thorns**, which are meant for defensive purposes. They are sub-epidermal in origin and may be either (a) simple, as in *Duranta plumieri* (Fam. Verbenaceae, Fig. 43, C), *Flacourtia sepiaria*



FIG. 43. THORNS

A, of *Carrisa* ; B, of *Aegle* ; C, of *Duranta* ; D, of *Flacourtia* ;
E, of *Hygrophila*.

(Fam. Bixaceae), sloe or black thorn (*Prunus spinosa*) of Fam. Rosaceae, *Hygrophila spinosa* (Fam. Acanthaceae, Fig. 43, E),

wood apple* (*Aegle marmelos*, Fig. 43, B) of Fam. Rutaceae, etc., (b) or compound, as in *Flacourtia cataphracta* (Fam. Bixaceae, Fig. 43, D), *Carissa carandus* (Fam. Apocynaceae, Fig. 43, A), *Randia dumetorum* (Fam. Rubiaceae), etc. That the thorns are metamorphosed stems is evident from the facts that they arise in the axils of leaves, often bear lateral branches and foliage leaves, and possess the characteristic internal structure of the stem.

Stem-tendrils (Fig. 44). In some climbing plants, the buds may be metamorphosed into tendrils. These are highly

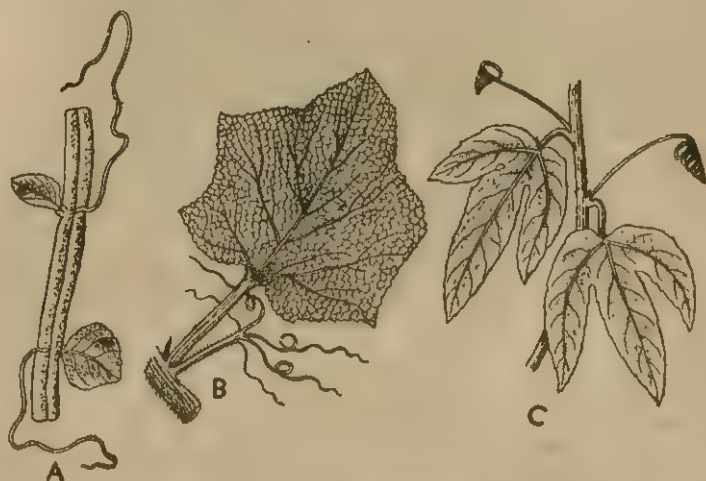


FIG. 44. STEM-TENDRILS
A, of *Vitis*; B, of *Cucurbita*; C, of *Passiflora*.

specialized climbing organs, which are very slender, simple or branched, thread-like structures and sometimes bear scale leaves. Tendrils are extremely sensitive to contact, and are capable of coiling round objects. These are usually axillary in position, as in passion flower (*Passiflora suberosa*, Fig. 44, C) of Fam. Passifloraceae. In *Vitis*† (Fig. 44, A), where the branching is of the sympodial type, the arrested terminal bud at the apex of each segment develops into a tendril, and assumes an apparently extra-axillary position. In *Cucurbita* (Fig. 44, B), the tendril is branched.

*The morphological nature of thorn in wood apple is, however, doubtful.
†*V. quadrangularis*, *V. pedata*, vine (*V. vinifera*), etc. of Fam. Vitaceae.

Phylloclade and cladode. In some cases, the stems, instead of being round, become more or less flattened, green in colour and take up the general appearance and functions of leaf. Under such conditions, in typical cases, the foliage leaves are either very small or wanting, or become modified into spines, while the flattened stems become more or less succulent, develop thick cuticle and are adapted in various ways for storing up water and cutting down transpiration. *Euphorbia antiquorum* (Fam. Euphorbiaceae), prickly pear (*Opuntia dillenii*, Fig. 45, A) of

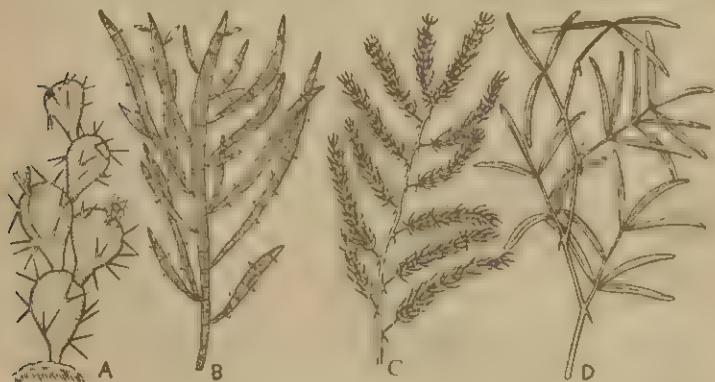
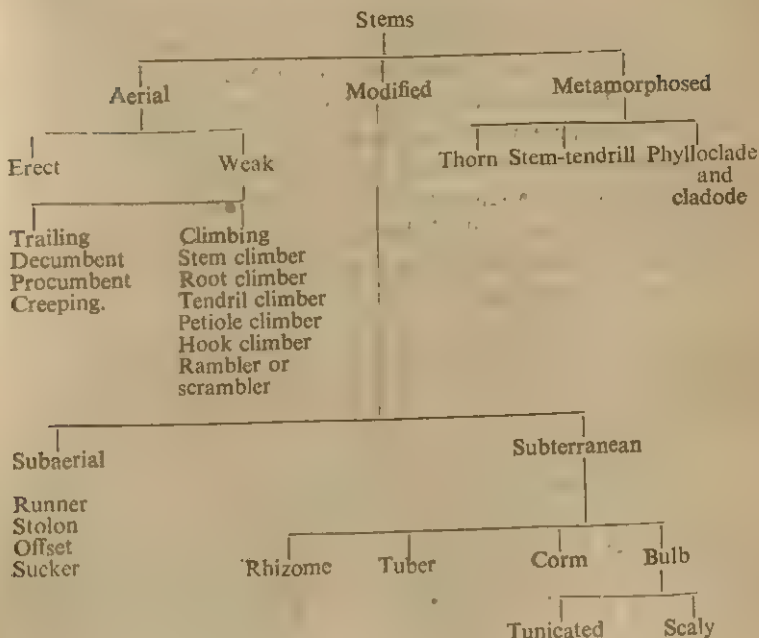


FIG. 45. PHYLLOCLADES AND CLADOSES

A, of *Opuntia* ; B, of *Muehlenbeckia* ; C, of *Tracemosus* ;
D, of *Asparagus* sp.

Fam. Cactaceae, *Muehlenbeckia platyclados* (Fig. 45, B) of Fam. Polygonaceae, whip tree (*Casuarina equisetifolia*) of Fam. Casuarinaceae, *Vitis quadrangularis* (Fig. 44, A) of Fam. Vitaceae, etc., are examples of such stems, known as **phylloclades**, which are usually found in dry districts and deserts. A phylloclade of one internode is a **cladode**, as in *Asparagus* (Fig. 45, C & D) of Fam. Liliaceae. The stem nature of the phylloclades and cladodes is evident from the facts that they arise in the axils of leaves, possess nodes and internodes (in case of phylloclades only), and often bear leaves and flowers.

The stems may be tabulated as follows :



FUNCTIONS OF STEMS

I. Normal functions. The normal functions of the stems are : (1) production and support of branches, leaves and reproductive structures (mechanical), and (2) conduction of absorbed solution and translocation of elaborated food (physiological).

II. Special functions. Besides the normal functions, stems also carry on other functions as stated below :

- (1) Storage of food, *e.g.*, Underground modified stems.
- (2) Storage of water, *e.g.*, Many cacti.
- (3) Assimilation, *e.g.*, Phylloclades and cladodes.
- (4) Vegetative propagation, *e.g.*, Subaerial and subterranean modified stems.
- (5) Self-defence, *e.g.*, Thorns of *Duranta*, wood apple, *etc.*
- (6) Climbing, *e.g.*, Stem-tendrils of grape.

BRANCHING

It has already been pointed out that the main stem, as it grows, either remains unbranched (as in palms), or gives rise to similar lateral members, the **branches**. These branches usually develop from the axillary buds or by the bifurcation of the apex (growing point) of the main stem. These secondary but similar members produce daughter branches in the same manner, and the process is continued until an elaborate **branch system** is produced. The manner in which these branches originate on the main stem constitutes the **branching**.

The branching is of two principal types (Fig. 46) :
(a) **dichotomous** and (b) **lateral**.

A. DICHOTOMOUS BRANCHING

The dichotomous branching takes place owing to the divided activity of the growing point of the main axis, thus producing two branches in a forked manner. The branches may or may not grow with equal vigour. The main axis thus forms the foot or the podium at the base of the fork, and the daughter branches may continue to divide in the same manner. This type of branching is found chiefly among the cryptogams.* The dichotomous branching may be of two kinds : (1) **normal** and (2) **sympodial**.

Normal or true dichotomy—In normal dichotomy, the tip bifurcates and gives rise to two equally vigorous daughter axes. These axes branch in their turn in the same manner. The best examples are seen in some of the pteridophytes, like *Psilotum triquetrum*, *Lycopodium clavatum*, and *Selaginella monospora*.

Sympodial dichotomy—When after bifurcation of the growing point, one of the daughter axes grows more rapidly than the other, which usually appears to be suppressed. The axis in this case is really a pseudo-axis. The sympodial dichotomy may again be either **helicoid**, i.e., one sided, or **scorpioid**, i.e., alternate-sided.

* Dichotomous branching is rarely found in some angiosperms, as in *Clinogyne dichotoma* (Fam. Cyperaceae).

B. LATERAL BRANCHING

The branching is said to be **lateral**, when the branches are always produced from the sides of the main axis due to the activity of its axillary buds. This type of branching is mainly characteristic of the angiosperms. The lateral branching is also of two kinds : (1) **racemose**, and (2) **cymose**.

Racemose or monopodial—When the primary axis continues to grow vigorously due to the activity of the terminal bud

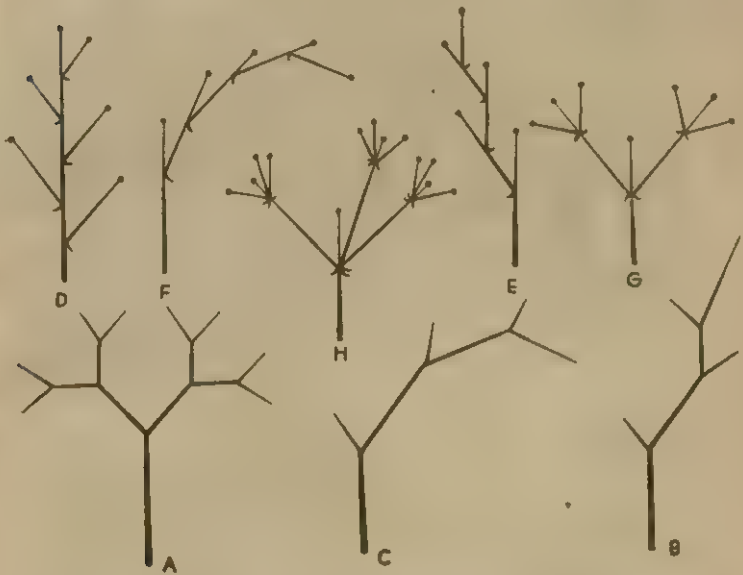


FIG. 46. BRANCHING

A, Normal dichotomy ; B, Scorpioid dichotomy ; C, Helicoid dichotomy ; D, Racemose ; E, Scorpioid cyme ; F, Helicoid cyme ; G, Biparous cyme ; H, Multiparous cyme.

and the branches are produced from the axillary buds in acropetal order of succession. In this case, the terminal bud persists throughout the life of the plant. This type of branching is also known as **monopodial**, because the primary axis forms the monopodium or the single foot, supporting the lateral branches. Familiar examples are common *Lawsonia alba* (Fam. Lythraceae, Fig. 48, A), *Polyalthia longifolia* (Fam. Anonaceae), pine (*Pinus longifolia*, a gymnosperm), etc.

Owing to the racemose type of branching, the shape of the tree becomes pyramidal or excurrent in form (Fig. 47, A).

Cymose or sympodial—Very frequently, the growth of the terminal bud is soon arrested, and one or more branches are produced from the axillary buds situated slightly below the



FIG. 47. LATERAL BRANCHING
A, Excurrent ; B, Doliquescent.

arrested terminal bud. In this case, the axillary buds grow more vigorously than the terminal one. Hence, the branches are more vigorous in their growth than the parent axis. These branches, in their turn, cease to grow, and give rise to others in similar manner. This type of branching is also known as **sympodial**, because the so-called axis is, in reality, not the parent axis but consists of the bases of several daughter axes, forming a false axis or **sympodium**.

Owing to the cymose type of branching, the shape of the tree becomes dome-shaped or *deliquescent* in form (Fig. 47, B), as in banyan (*Ficus benghalensis*) and jack (*Artocarpus integrifolia* = *A. integrifolia*) of Fam. Moraceae, mango (*Mangifera indica*) of Fam. Anacardiaceae, etc.

According to the number of branches produced below the arrested terminal bud, the cymose branching may be classified as follows.

Uniparous, i.e., when only one branch is produced. If the successive daughter axes are produced alternately right and left in a zig-zag manner, the branching is said to be *scorpioid*, as in *Vitis quadrangularis* of Fam. Vitaceae, but if they are developed on one side only, it is said to be *helicoid*, as in *Saraca indica* of S.F. Caesalpiniaceae (Fam. Leguminosae).

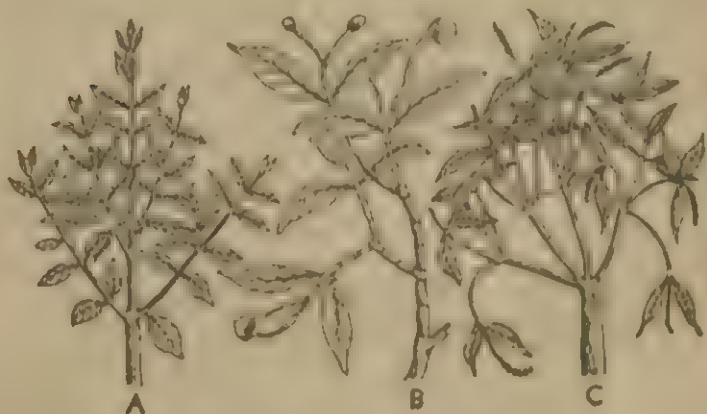


FIG. 48. BRANCHING

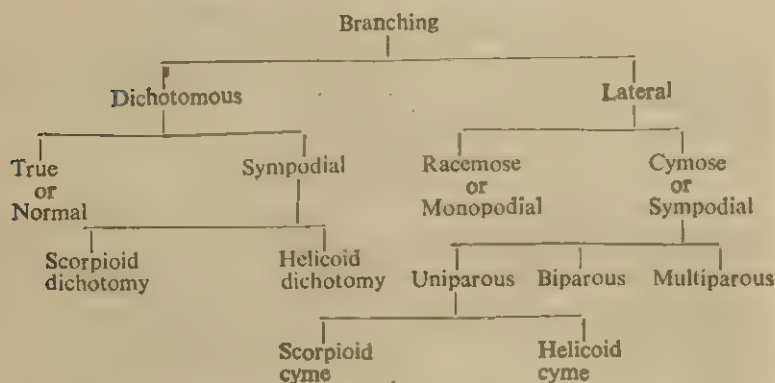
A, Racemose of *Lawsonia*. B, Biparous cyme of *Levetamia*.
C, Multiparous cyme of *Croton*

Biparous, i.e., when two daughter branches are produced, as in marvel of Peru (*Mirabilis Jalapa*) of Fam. Nyctaginaceae, *Levetamia indica* (= *Tabernaemontana coronaria*, Fig. 48, B), and *Carissa carandas* of Fam. Apocynaceae, etc. Sometimes, in this type of branching the terminal bud soon dies down, and the two lateral branches appear, as if caused by a splitting of the terminal bud, and look like a dichotomy, such a branching is known as the *false dichotomy*, as in temple tree (*Plumeria acutif-*

folia) of Fam. Apocynaceae, mistletoe (*Viscum album*) of Fam. Loranthaceae, and some cacti (Fam. Cactaceae), etc.

Multiparous, i.e., when more than two daughter branches are produced, as in *Croton sparciflorus* (Fam. Euphorbiaceae, Fig. 48, C).

The branching may be tabulated as follows :



ECONOMIC IMPORTANCE OF STEMS

The economic products obtained from the stems of plants cover a very wide range and serve many useful purposes. One of the most important foods derived from the stem is sugar, which is obtained from the sap of the sugarcane plant. All the underground stems serve as important human foods. The rhizomes of turmeric (*Curcuma longa*) and mango ginger (*Curcuma amada*) of Fam. Zingiberaceae are used as condiments, while that of Indian arrowroot (*Curcuma zeodoria*) yields an inferior kind of arrowroot. The various kinds of valuable timber are stem products. Ordinary wood, used as fuel, is also derived from the stem ; this is also a source of cheap quality of paper. The stems of plants, like jute (*Corchorus capsularis* and *C. olitorius*) of Fam. Tiliaceae, flax (*Linum usitatissimum*) of Fam. Linaceae, hemp (*Hibiscus cannabinus*) of Fam. Malvaceae, etc., furnish us with fibres, utilized for the manufacture of clothings, gunny bags and other commercial

commodities. Various kinds of chemicals and dye-stuffs are obtained from the stems. Medicine, like quinine, is obtained from the bark of stems of *Cinchona officinalis*, *C. succirubra*, *C. ledgeriana* and *C. calisaya* of Fam. Rubiaceae. The stem-tubers of *Cyperus rotundus* and *Scirpus grossus* of Fam. Cyperaceae as well as the rhizomes of ginger (*Zingiber officinale*) of Fam. Zingiberaceae are also used in medicines. Cinnamon is a product of the stem-bark of *Cinnamomum zeylanicum* (Fam. Lauraceae). Rubber, latex and guttapercha are obtained by tapping stems of various plants. Gums, resins, balsams and their products are secretions of the stems. From the pith of sago palm (*Metroxylon rumphii*) of Fam. Palmae is obtained the sago of commerce. The stem-bark of *Broussonetia papyrifera* (Fam. Moraceae) is used for paper-making in Japan.

CHAPTER III

THE LEAF

Leaves are the dissimilar lateral members of the stem or the branch, and bear buds in their axils. They are developed from the nodes in acropetal order, are of limited growth and exogenous in origin, and are usually characterized by their expanded forms, green colour and dorsiventral nature. But these characters may vary depending on the various environmental conditions for serving different purposes.

DURATION OF LEAVES

According to their duration, leaves may be considered as belonging to either of the following categories.

Fugacious or caducous—when the leaves fall off very soon after their development, as in *Acacia recurva* of S.F. Mimosae (Fam. Leguminosae).

Deciduous or annual—when the leaves remain for one growing season and then fall off, as in banyan (*Ficus benghalensis*) of Fam. Moraceae, silk cotton tree (*Salmaaliala malabarica*=*Bombax malabaricum*) of Fam. Bombacaceae, hog plum (*Spondias mangifera*) of Fam. Anacardiaceae, etc.

Persistent or perennial or evergreen—when the leaves persist on the stem for more than one seasons, as in mango (*Mangifera indica*) of Fam. Anacardiaceae, jack (*Artocarpus integra*=*A. integrifolia*) of Fam. Moraceae, etc. It is to be noted that all the leaves do not fall off at a time, but are shed throughout the year.

KINDS OF LEAVES

The leaves of angiosperms show a great diversity in their forms and functions. They are of the following kinds.

Cotyledons or seed leaves. These are the leaves of the embryo. Their leaf nature, various forms and functions have been discussed in detail in Chapter XI.

Scale leaves or scales or cataphylls. These leaves are usually non-green, and in most cases appear brownish in colour. These are usually inconspicuous, thin and membraneous (as found on rhizomes, tubers, etc.), but may become fleshy owing to the accumulation of food (as in bulbs) and are usually attached to the stem by a relatively broad base, and possess buds in their axils. Scale leaves are invariably sessile, often much reduced and represented by the leaf-base only. In case of plants possessing underground stems, the scale leaves precede the development of ordinary foliage leaves, and various transitional forms in between the two may be noticed. In some cases, these are green in colour and occur on the aerial shoots, as in young bamboo (*Bambusa arundinacea*) of Fam. Gramineae, or may protect the terminal bud as bud-scales, as in *Michelia champaca* and *Magnolia grandiflora* of Fam. Magnoliaceae, banyan (*Ficus benghalensis*) and jack (*Artocarpus integra* = *A. integrifolia*) of Fam. Moraceae, etc. In whip tree (*Casuarina equisetifolia*) of Fam. Casuarinaceae, horsetail (*Equisetum arvense*, a pteridophyte) etc., the scales occur in whorls at the nodes. Their main function is to protect the axillary as well as terminal buds.

Foliage leaves or prophylls. These are the green, expanded leaves of the aerial shoots and are very important to the life of a plant, since these are the chief organs of photosynthesis, respiration and transpiration. Foliage leaves are usually *cauline*, as these are developed on the main stem or its branches. Occasionally, however, these are produced from apparently stemless plants forming rosettes; such leaves are called *radical*, as in radish (*Raphanus sativus*) of Fam. Cruciferae, carrot (*Daucus carota*) of Fam. Umbelliferae, etc.

Bract leaves or bracts or hypsohylls. These are simpler and usually smaller than the foliage leaves, and bear flowers or floral axes in their axils. Their main function is either protection or attraction of insects to bring about pollination. Bracts may be of various kinds as discussed below.

(a) **Leafy**, when the bracts are green and leaf-like in appearance, as in *Acalypha indica* (Fam. Euphorbiaceae).

(b) **Petaloid**, when brightly coloured, as in *Poinsettia*

pulcherrima (Fam. Euphorbiaceae), glory of garden (*Bougainvillea spectabilis*, Fig. 49, A) of Fam. Nyctaginaceae, etc.

(c) **Spathe**, when large, often brightly coloured and enclosing an inflorescence, as in common arum (*Colocasia antiquorum*, Fig. 49, B) of Fam. Araceae, palms of Fam. Palmae, or part of an inflorescence, as in banana (*Musa paradisiaca* var. *sapientum*) of Fam. Musaceae.

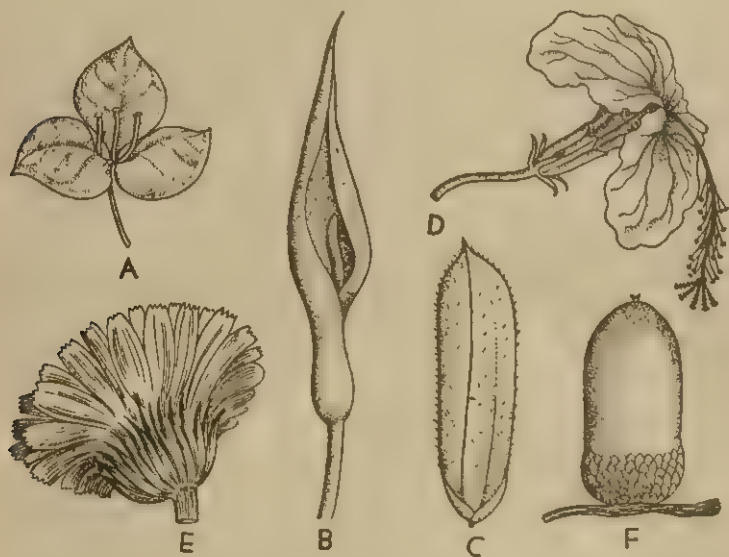


FIG. 49. DIFFERENT KINDS OF BRACTS

A, Petaloid of *Bougainvillea* ; B, Spathe of *Colocasia* ; C, Glumes and palea of *Oryza* ; D, Epicalyx of *Hibiscus* ; E, Involucre of a composite ; F, Cupule of *Quercus*.

(d) **Glume**, when thin, dry and scaly, as in wheat (*Triticum aestivum* T. *vulgare*), paddy (*Oryza sativa*, Fig. 49, C) and grasses of Fam. Gramineae.

(e) **Palea**, when chaff-like, as in some plants belonging to Fams. Gramineae (Fig. 49, C) and Compositae.

(f) **Epicalyx**, when a single whorl of minute, leaf-like structures occurs below the calyx, as in China rose (*Hibiscus rosa-sinesis*) of Fam. Malvaceae (Fig. 49, D).

(g) **Involucre**, when two or more whorls of bracts occur

underneath an inflorescence and become partly or completely united, as in members belonging to Fam. Compositae (Fig. 49, E). In Umbelliferae, the involucre are rather minute, and are known as *involucels*.

(h) **Cupule**, when the bracteoles (minute bracts) fuse, subsequently enlarge during the formation of fruit, and form a cup-like structure round it, as in birch (*Betula bhojpatra*) and oak (*Quercus spicata*, Fig. 49, F) of Fam. Cupuliferae, *Taxus baccata* (a gymnosperm), etc.

Floral leaves. These are specialized leaves of a flower, which constitute sepals, petals, stamens and carpels. These will be fully discussed in connection with the flower (Chapter V).

PARTS OF A TYPICAL LEAF (Fig. 50)

A typical leaf consists of the following three parts :

(1) **Epipodium or lamina or leaf-blade.** It is the terminal portion of the leaf, and is normally a thin, green expanded portion.

(2) **Mesopodium or petiole or leaf-stalk.** It is a more or less cylindrical rod-like structure supporting the lamina.

(3) **Hypopodium or leaf-base.** It is that portion of the leaf by means of which it is attached to the stem or branch.

The epipodium, mesopodium and hypopodium together constitute the **phyllodium**. When any one of these parts is wanting, the leaf is said to be **incomplete**.

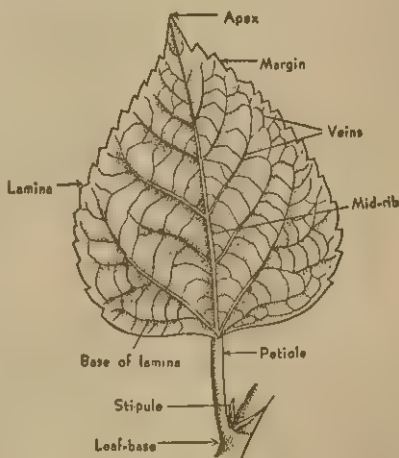


FIG. 50. PARTS OF A TYPICAL LEAF

The leaf may be studied separately with reference to its three parts.

I. THE LEAF-BASE OR HYPOPODIUM

Sometimes it becomes extremely difficult to delimit the leaf-base from the petiole, when the latter is poorly developed. When it becomes distinctly swollen, as in mango (*Mangifera indica*) of Fam. Anacardiaceae, sensitive plant (*Mimosa pudica*) of S.F. Mimosae (Fam. Leguminosae), etc., usually forming a sort of cushion, it is known as the **pulvinus**. Occasionally, however, the base broadens out into a flattened structure forming a sheath round the stem, either completely (**amplexicaul**), as in *Dendrocalamus* and a few grasses of Fam. Gramineae, or partially (**semi-amplexicaul**), as in palms. These are known as **sheathing leaf-bases**, which are usually found among the monocotyledons, but are also illustrated by many plants of the families Ranunculaceae, Dilleniaceae, Umbelliferae and Araliaceae among the dicotyledons. It is interesting to note that in plants, like banana (*Musa paradisiaca* var. *sapientum*) and traveller's tree (*Revenala madagascariensis*) of Fam. Musaceae, the so-called stem is formed by the sheathing leaf-bases only. In the leaves of the members of the Fam. Gramineae, the sheath is split open on the side of the stem opposite the lamina, and scaly structures, known as **ligules**, are found at the junction of the lamina and the sheath. But in the Fam. Cyperaceae, the sheath is completely closed and the ligule is absent. The leaf-base either gives protection to the axillary bud or supports the base of the internode, when sheathing. In some of the dicotyledonous plants and rarely in monocotyledonous ones, the leaf bears a pair of lateral outgrowths, known as **stipules**.

THE STIPULES

The stipules are lateral appendages of the leaf-base and usually occur in pairs. There are, however, plants in which they are absent. In the monocotyledonous plants, the stipules are very rare. Leaves with stipules are called **stipulate** leaves, and those without them are called **exstipulate** ones, as in guava (*Psidium guayava*) of Fam. Myrtaceae, mango (*Mangifera indica*) of Fam. Anacardiaceae, litchi (*Litchi chinensis*) of Fam. Sapindaceae, custard apple (*Anona squamosa*) of Fam. Anonaceae, etc. In many plants, the stipules are very small and often overlooked.

They vary widely in shape, colour, size and position, and often form important morphological units from the standpoint of Systematic Botany.

Stipules are **persistent**, when they remain as long as the lamina is attached to the stem, as in rose (*Rosa centifolia*) off Fam. Rosaceae, or **deciduous**, when they fall off soon after the unfolding of the leaf from the bud condition, as in *Dillenia indica* (Fam. Dilleniaceae). In still other cases, they fall off before the leaf unfolds, as in *Michelia champaca* (Fam. Magnoliaceae), jack (*Artocarpus integra* = *A. integrifolia*), banyan (*Ficus benghalensis*) of Fam. Moraceae, etc. ; such stipules are said to be **caducous**.

FORMS OF STIPULES (Fig. 51)

The stipules are of different forms as described below.

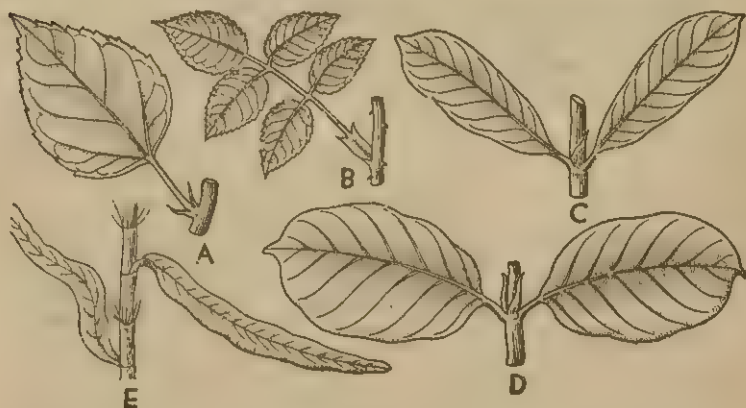


FIG. 51. STIPULES

A, Free and lateral of *Hibiscus* ; B, Adnate of *Rosa* ; C, Intrapetiolar of *Gardenia* ; D, Interpetiolar of *Ixora* ; E, Ochreate of *Polygonum*.

Free and lateral—when there are two distinct filiform stipules, on the two sides of the leaf-base, as in China rose (*Hibiscus rosa-sinensis*, Fig. 51, A), cotton (*Gossypium herbaceum*) and other plants belonging to Fam. Malvaceae. They are also found in Fams. Sterculiaceae, Tiliaceae, Leguminosae, Euphorbiaceae, etc.

Adnate—when the stipules are attached to the sides of

the petiole for some distance, as in rose (*Rosa centifolia*, Fig. 51, B) and other plants belonging to Fam. Rosaceae.

Intrapetiolar or **axillary** when the stipules of opposite leaves unite by their inner margins and lie in the axils of leaves, as in *Gardenia florida* (Fig. 51, C) and *Poederia foetida* of Fam. Rubiaceae.

Interpetiolar when the union takes place between the outer margins of the stipules of opposite or whorled leaves, and these united structures lie in between the leaf-bases, as in *Toora coccinea*, *T. parviflora* (Fig. 51, D), *Anthocephalus cadamba* and some other plants of Fam. Rubiaceae, *Stychnos nuxvomica*, *S. potatorum* and other plants of Fam. Loganiaceae.

Ochreate when the stipules of alternate leaves are united both by their inner and outer margins to form a tubular sheath (**ochrea**) round the base of each internode, as in *Polygonum barbatum* (Fig. 51, E), *P. orientale*, dock (*Rumex vesicarius*) and most of the plants of Fam. Polygonaceae, rattan palm (*Calamus rotang*), and *Korthalsia scaphigera*, a Malayasian scrambler, both of Fam. Palmae, etc.

MODIFIED STIPULES

The stipules may be modified as follows:

Foliateous when the stipules are large, green and leaf-like as in pea (*Pisum sativum*, Fig. 52, A) and wild pea (*Lathyrus aphaca*, Fig. 79, F) of S.F. Papilionaceae (Fam. Leguminosae).

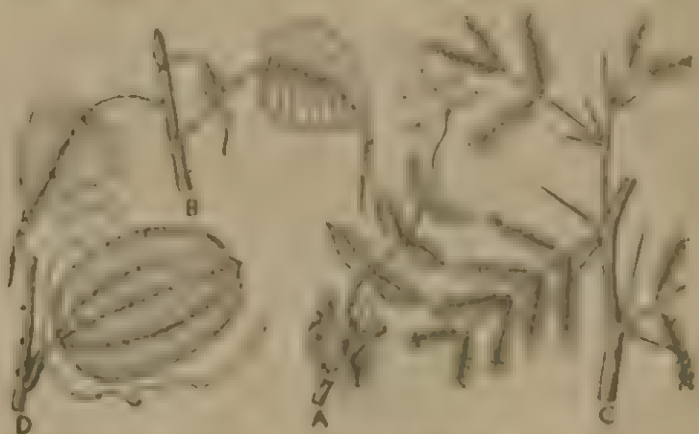
Winged when the stipules are expanded into wing-like structures, as in *Crotalaria alata* of S.F. Papilionaceae (Fam. Leguminosae).

Consolute stipules or **bud-scales** when the stipules form pale membranous protective structures covering the buds, and fall off as the leaves unfold, as in banana (*Musa benenaluensis*), twisted peepul (*Ficus religiosa*, Fig. 52, B), jack (*Artocarpus integrifolia* = *A. integrifolia*), and other plants of Fam. Moraceae. *Morinda chinensis*, *Magnolia grandiflora* and other plants of Fam. Magnoliaceae.

Tendrillar when the stipules are modified into tendrils, as in sarapapilla (*Smilax macrophylla*, Fig. 52, D) of Fam. Liliaceae.

Spin, when the stipules are modified into spines or in stative part (*Mimosa pudica* and *Acacia drepanoloba* (fig. 5), 6) of SE. Mimosa (from *Leguminosae*, to also *Ulex europaeus* of Fab. *Rhizobium*, etc.

Stipules are usually simple but may be divided, as do *Leptocarpus* and *Chamaecrista*. When stipular outgrowths develop at the base of the leaflets of a com-



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A. The Ca^{2+} concentration in the Ca^{2+} solution is 10^{-4} M . The Ca^{2+} concentration in the Ca^{2+} solution is 10^{-4} M .

ground leaf, these are known as *stipels*, as in *Dermatium*
gambellum and bean (*hemilobus* of S. Papilionaceae (Fab-
 Leguminosae).

I have been thinking of you a great deal lately. I hope you are well and happy. I have been very busy lately, but I have managed to find some time to write to you. I have been thinking of you a great deal lately. I hope you are well and happy. I have been very busy lately, but I have managed to find some time to write to you.

As to the function, the stipules are mainly protective structures, either protecting the axillary buds from being injured or protecting the most tender leaves in bud-stages. When large and

foliaceous, these act as photosynthetic organs. As spiny and tendrillar stipules, these are defensive and climbing organs respectively ; sometimes the stipules secrete mucilage for the protection of buds.

II. THE LEAF-STALK OR PETIOLE OR MESOPODIUM

This is the slender rod-like structure supporting the lamina at its base. But occasionally, as in lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae, garden nasturtium (*Tropaeolum majus*) of Fam. Tropaeolaceae, etc., the petiole is attached to the back of the lamina ; such a leaf is said to be a **peltate** one. A leaf possessing petiole is known as a **petiolate** leaf, as in mango (*Mangifera indica*) of Fam. Anacardiaceae, banyan (*Ficus benghalensis*) of Fam. Moraceae, etc., and that without it, **sessile**, as in Mexican poppy (*Argemone mexicana*) of Fam. Papaveraceae, glory lily (*Gloriosa superba*) of Fam. Liliaceae, *Canscora decussata* (Fam. Gentianaceae), pink (*Dianthus chinensis*) of Fam. Caryophyllaceae, etc. When present, the petiole may be short or long, more or less cylindrical in structure and its upper surface may be slightly flattened or grooved, as in banana (*Musa paradisiaca* var. *sapientum*) of Fam. Musaceae, or hollow, as in papaw (*Carica papaya*) of Fam. Caricaceae.

MODIFIED PETIOLES (Fig. 53)

Winged petiole. Sometimes, the petiole becomes distinctly flattened and winged, as in *Pothos cathcartii* (Fam.

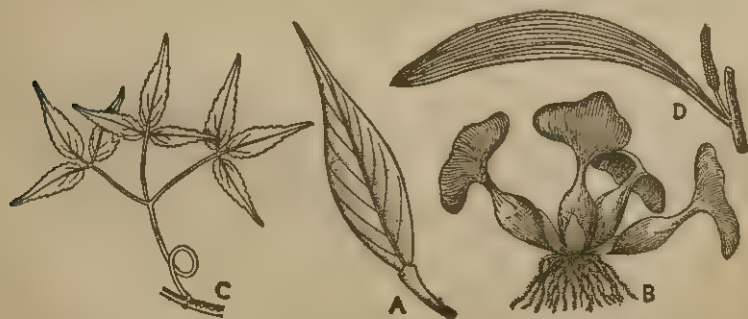


FIG. 53. MODIFIED PETIOLES

A, Winged petiole ; B, Swollen petiole ; C, Twisting petiole ; D, Phyllode.

Araceae (Fig. 53, A), *Citrus* sp. (Fam. Rutaceae), etc. According to some, the flattened, leaf-like structure of the pitcher plant (*Nepenthes* sp.) of Fam. Nepenthaceae, is also a winged petiole.

Swollen petiole. Sometimes, in water plants the petiole is provided with a mass of spongy tissue, which helps the plant in floating, as in water hyacinth (*Eichhornia crassipes*, Fig. 53, B) of Fam. Pontederiaceae, water chestnut (*Trapa bispinosa*) of Fam. Onagraceae, etc.

Twisting petiole. Sometimes, the petiole coils round the neighbouring objects and helps the plant in climbing, as in virgin's bower (*Clematis gouriana*, Fig. 53, C) of Fam. Ranunculaceae, *Aristolochia indica* (Fam. Aristolochiaceae), etc.

Phyllode. Sometimes, the lamina does not develop at all, as in *Acacia moniliformis* of S.F. Mimosae (Fam. Leguminosae, Fig. 53, D), and *Phyllarthorn commorensense* (Fam. Bignoniaceae), or falls off at an early stage of its development, as in *A. recurva*; the petiole in such cases becomes flattened in a vertical plane and takes up the function and appearance of the lamina. Such a modified petiole is known as a **phyllode**.

Spine. Sometimes, the blades fall off when mature, leaving behind the petioles, which grow into rigid spines, as in Rangoon creeper (*Quisqualis malabaricum*) of Fam. Combretaceae.

The function of the petiole is to conduct materials to and from the lamina. By its growth, as well as bending and twisting power, the petiole brings the lamina in proper position to secure adequate sunlight. When flat and green, it carries on photosynthesis either partly or wholly. When swollen, it helps the plant in floating.

THE PHYLLODE THEORY

De Candolle (1827) suggested that the linear type of a monocotyledonous leaf is to be regarded as equivalent to the leaf-base and the leaf-stalk of a dicotyledonous leaf, the leaf-blade remaining wanting. This idea of de Candolle later on came to be known as the *phyllode theory* of the monocotyledonous leaf. Arber is an ardent supporter of this idea.

In general a monocotyledonous leaf can be easily distinguished from a dicotyledonous one by means of studying the external appearance of the two leaves. In the former, the venation is usually parallel, while in the latter it is reticulate. One of the characteristic features found in a number of families of monocotyledons is the particular leaf type in which the leaf-base is sheathing in nature, which gradually passes into the laminar portion. Though the condition is very much different in case of dicotyledonous leaves, yet some of these, which are known as the 'reduced' leaves, make an approach to the monocotyledonous condition. Such leaves either do not possess any lamina at all or just a midrib represents the same. In *Oreomyrrhis linearis* (Fam. Umbelliferae) the elongated leaf-base practically makes up the entire body of the leaf, while the rest of it is reduced to a minute hood-like structure. In *Acacia moniliformis* and *A. recurva* of S.F. Mimosae, as well as in *Clematis asfoliata* (Fam. Ranunculaceae) and *Oxalis bupleurifolia* (Fam. Oxalidaceae) the petiolar phyllode is the most conspicuous part of the leaf, the lamina being entirely wanting in a mature leaf. Arber points out that there are a number of monocotyledonous leaves which can be interpreted as petiolar phyllodes from their morphological appearance as well as internal structure. For example, a close series of anatomical parallels can be detected among the phyllodes of some species of *Acacia* and the isobilateral leaves of the members of the family Iridaceae. In these the bundle of the midrib becomes inconspicuous while the two main lateral veins come into prominence and give rise to a pseudo-midrib.

It is rather easy to apply the phyllode theory to the radial and ensiform (grass-like) types of leaves, but it is somewhat difficult to do the same where the leaves are ribbon-like in appearance with a single series of vascular bundles, as in *Cymodocea nodosa* (Fam. Potamogetonaceae), *Triglochin procerum* (Fam. Juncaginaceae), etc. But, here also Arber has established the relationship between such ribbon-like leaves with solid phyllode-like leaves. For example, in three species of *Cymodocea* three different leaf types are noted; in *C. isoetifolia* the leaves are of the radial type, in *C. nodosa* these are ribbon-like, while an intermediate condition is to be found in *C. manatorum*.

In *Asparagus racemosus* (Fam. Liliaceae) a very much

reduced type of leaf can be seen. Here there are scale leaves with a spine at the base and these are pointed downwardly. Arber interprets, on anatomical grounds, the scale as some sort of ligular sheath and the spine as the phyllode.

A further elaboration of the petiole forming lamina-like structures is shown by the leaves of some members of the families *Palmaceae* and *Iridaceae*. Serial sections taken through the young embryonic leaves of *Cocos* and *Trachycarpus*, both belonging to the Fam. *Palmae*, reveal that the sheathing leaf-base is always followed by a short petiolar portion. A series of invaginations penetrates within the tissues in between the vascular bundles, and gives rise to a 'pseudo-lamina'. Finally, this fan-shaped body expands and the typical fan- or feather-like leaf is formed by secondary splittings. On the basis of the phyllode theory, such leaves are, therefore, not true laminae but are only the elaborations of the petiolar distal regions. In *Crocus* (Fam. *Iridaceae*) the leaf is developed from a solid petiole by two invaginations only.

The phyllode theory has been found to be advantageous, since it does not only explain parallel venation but also the derivation of cordate types of leaves (found in some monocotyledons) from parallel-veined organs.

III. THE LEAF-BLADE OR LAMINA OR EPIPODIUM

In general, it is the most important and conspicuous part of the leaf. But as an adaptation to extremes of climate, it may be reduced, modified or even absent. It is, as a rule, thin, usually dorsiventral, and is constructed in such a way as to expose the largest photosynthetic surface to sunlight. The lamina is always traversed by a system of strong network consisting of nerves or veins, which anastomose in various ways. These veins are the branches of the midrib (main vein), which runs through the middle of the lamina from its base to the apex.*

*Usually, the midrib divides the lamina into two equal halves, but in some cases, the halves are unequal; the latter kind of leaves are said to be asymmetrical ones, as in members of Fams. *Meliaceae*, *Bignoniaceae*, *Nyctaginaceae*, etc.

The lamina presents wide variations as regards its general outline, margin and other characters, though these are, in most cases, constant for any particular species. These are also important for systematic purposes, and to describe them accurately, it is necessary for the sake of convenience to discuss the following heads : (a) general outline, (b) apex, (c) margin, (d) base, (e) surface, (f) texture, and (g) venation.

GENERAL OUTLINE OF LAMINA (Fig. 54)

(a) *With lamina nearly of the same width throughout*

Acicular or needle-shaped, when the lamina is long, very narrow and sharp-pointed, as in pine (*Pinus longifolia*, a gymnosperm, Fig. 54, 1).

Linear, when the lamina is long, flat and very narrow with nearly parallel margins, as in tuberose (*Polianthes tuberosa*, Fig. 54, 2) of Fam. Amaryllidaceae, and many grasses.

Lanceolate or lance-shaped, when the lamina is comparatively narrow but broadest in the middle or a little below, and tapering towards both the apex as well as the base, as in oleander (*Nerium odorum*, Fig. 54, 3) of Fam. Apocynaceae, custard apple (*Anona squamosa*) and mast tree (*Polyalthia longifolia*) of Fam. Anonaceae, *Polygonum orientale* (Fam. Polygonaceae), bamboo (*Bambusa arundinacea*) of Fam. Gramineae, *Butomopsis lanceolata* (Fam. Alismataceae), etc.

Oblong, when the lamina is flat and broad with margins parallel but obtuse or rounded at the apex, as in banana (*Musa paradisiaca* var. *sapientum*, Fig. 54, 4) of Fam. Musaceae.

(b) *With lamina widest near the base*

Subulate or awl-shaped, when the lamina is narrow, firm and gradually tapers from base to apex, as in saltwort (*Salsola kali*) of Fam. Chenopodiaceae, *Thuja occidentalis* (a gymnosperm), *Isoetes* (a pteridophyte), etc.

Ovate or egg-shaped, when the base of the lamina is broadest, resembling an egg, as in China rose (*Hibiscus rosa-sinesis*, Fig. 54, 5) of Fam. Malvaceae, banyan (*Ficus benghalensis*) of Fam. Moraceae, *Anisomeles ovata* (Fam. Labiatae), *Solanum*

nigrum (Fam. Solanaceae), *Acalypha indica* (Fam. Euphorbiaceae), etc.

Cordate or heart-shaped, when the base of the lamina is broad but with a deep notch, so as to form two lobes and a pointed apex, as in betel vine (*Piper betle*, Fig. 54, 6) of Fam. Piperaceae, *Tinospora cordifolia* (Fam. Menispermaceae), *Sida cordifolia*

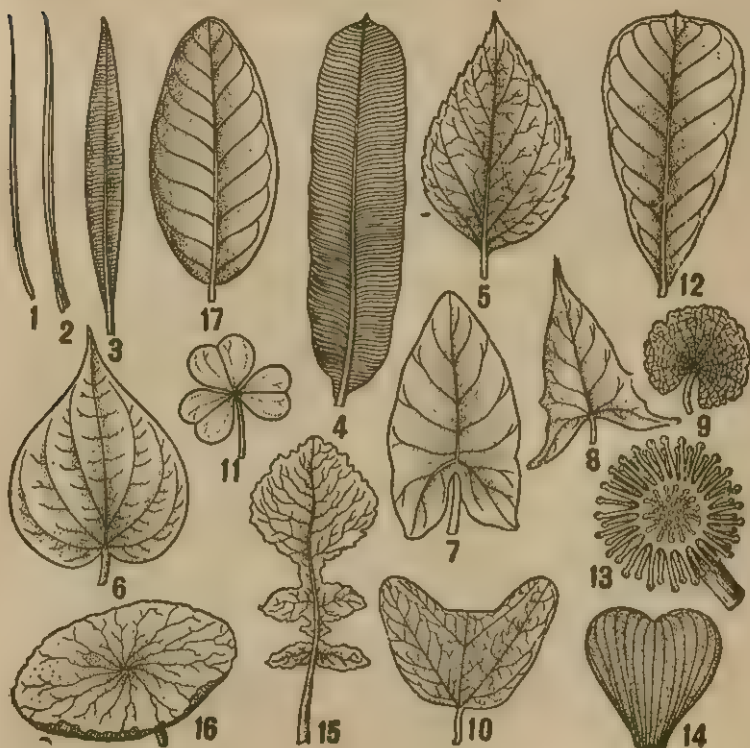


FIG. 54. GENERAL OUTLINE OF LAMINA

1, Acicular ; 2, Linear ; 3, Lanceolate ; 4, Oblong ; 5, Ovate ; 6, Cordate ; 7, Sagittate ; 8, Hastate ; 9, Reniform ; 10, Lunate ; 11, Obcordate ; 12, Obovate ; 13, Spathulate ; 14, Cuneate ; 15, Lyrate ; 16, Orbicular ; 17, Elliptical.

and *Abutilon indicum* of Fam. Malvaceae, madder (*Rubia cordifolia*) of Fam. Rubiaceae, *Pedilanthus tithymaloides* (Fam. Euphorbiaceae), *Argyrea speciosa* (Fam. Convolvulaceae), etc.

Sagittate or arrow-shaped, when the two lobes of the laminar base are directed downwards with pointed apex, as in arrow-head (*Sagittaria sagittifolia*, Fig. 54, 7) and *Limnophyton* sp. of Fam. Alismataceae, toad flax (*Linaria ramosissima*) of Fam. Scrophulariaceae, *Ipomoea reptans* (Fam. Convolvulaceae), etc.

Hastate or dart-shaped, when the two lobes of the basal part of a lamina are directed outwards with pointed apex, as in *Typhonium trilobatum* (Fig. 54, 8) of Fam. Araceae.

Reniform or kidney-shaped, when the lamina is as in the cordate one, but the apex is rounded, as on Indian pennywort (*Hydrocotyle asiatica*, Fig. 54, 9) of Fam. Umbelliferae.

Lunate or crescent-shaped, when the two pointed lobes of the lamina are directed outwards and it resembles the shape of the half-moon, as in *Passiflora lunate* (Fam. Passifloraceae, Fig. 54, 10), *Adiantum lunatum* (a pteridophyte), etc.

(c) *With lamina widest near the apex*

Obcordate or heart-shape reversed, as in *Bauhinia variegata* of S.F. Caesalpiniae (Fam. Leguminosae), wood sorrel (*Oxalis corniculata*, Fig. 54, 11) of Fam. Oxalidaceae, etc.

Obovate or egg-shape reversed, as in jack (*Arotocarpus integra*=*A. integrifolia*, Fig. 54, 12) of Fam. Moraceae, country almond (*Terminalia catappa*) of Fam. Combretaceae, *Finlaysonia obovata* (Fam. Asclepiadaceae), *Cassia obovata* of S.F. Caesalpinieae (Fam. Leguminosae), etc.

Spathulate or spatula-shaped, when the apex is broad and rounded and gradually tapering towards the base, as in *Euphorbia nerifolia* (Fam. Euphorbiaceae), *Duranta plumieri* and *Lippia nodiflora* of Fam. Verbenaceae, sundew (*Drosera burmanni*, Fig. 54, 13) of Fam. Droseraceae, *Kalanchoe spathulata* (Fam. Crassulaceae), etc.

Cuneate or wedge-shaped, when the apex is broad and flattened and tapering to the base but with a more or less acute apex, as in water lettuce (*Pistia stratiotes*, Fig. 54, 14) of Fam. Araceae.

Lyrate or lyre-shaped, when the apex has a large oval terminal lobe and two or more gradually smaller lobes resembling a lyre, as in mustard (*Brassica nigra*) and radish (*Raphanus sativus*, Fig. 54, 15) of Fam. Cruciferae.

(d) With lamina symmetrical

Orbicular, when the lamina is circular in outline or nearly so, as in lotus (*Nelumbo nucifera*—*Nelumbium speciosum*, Fig. 54, 16) of Fam. Nymphaeaceae, garden nasturtium (*Tropaeolum majus*) of Fam. Tropaeolaceae, etc.

Elliptical, when the lamina is like an ellipse, as in periwinkle (*Vinca rosea*, Fig. 54, 17) of Fam. Apocynaceae, India rubber (*Ficus elastica*) of Fam. Moraceae, *Mimusops elengi* (Fam. Sapotaceae), etc.

APEX OF LAMINA (Fig. 55)

The apex of the lamina may be :

Acute or pointed, as in China rose (*Hibiscus rosa-sinensis*) and *Sida acuta* of Fam. Malvaceae, *Corchorus acutangularis* (Fig. 55, B) of Fam. Tiliaceae, *Barringtonia acutangula* of Fam. Lecythidaceae, *Plumeria acutifolia* (Fam. Apocynaceae), etc.

Acuminate, when slender and much prolonged like a tail, as in peepul tree (*Ficus religiosa*, Fig. 55, C) of Fam. Moraceae, *Bauhinia acuminata* of S.F. Caesalpinieae (Fam. Leguminosae), etc.

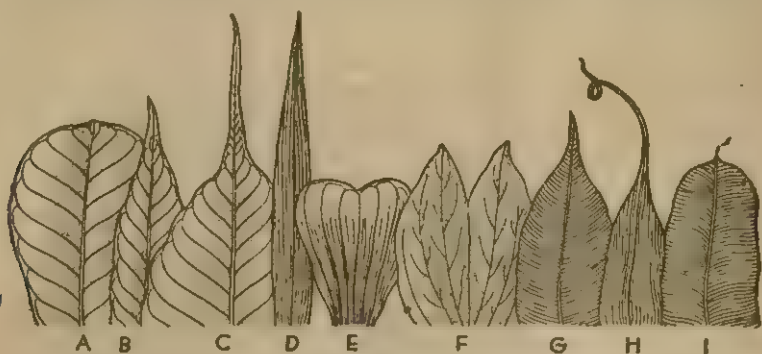


FIG. 55. APEX OF LAMINA

A, Obtuse ; B, Acute ; C, Acuminate ; D, Cuspidate ; E, Retuse ; F, Emarginate ; G, Mucronate ; H, Tendrillar ; I, Cirrhose.

Cuspidate or spiny, when the apex ends in a hard, rigid point, as in date (*Phoenix sylvestris*, Fig. 55, D) of Fam. Palmae, *Agave cantula* (Fam. Amaryllidaceae), *Jacquinia ruscifolia* (Fam. Myrsinaceae), etc.

Obtuse or rounded, as in jack (*Artocarpus integra*=*A. integrifolia*, Fig. 55, A) of Fam. Moraceae, country almond (*Terminalia catappa*) of Fam. Combretaceae, etc.

Retuse, when the obtuse apex is slightly notched, as in water lettuce (*Pistia stratiotes*, Figs. 54, 14 & 55, E) of Fam. Araceae, *Clitoria ternatea* of S.F. Papilionaceae (Fam. Leguminosae), etc.

Emarginate, when the obtuse apex is deeply notched, as in wood sorrel (*Oxalis corniculata*, Fig. 54, 11) of Fam. Oxalidaceae, *Bauhinia variegata* (Fig. 55, E) of S.F. Caesalpinieae (Fam. Leguminosae), etc.

Mucronate, when the obtuse apex abruptly ends in a small and short point, as in India rubber (*Ficus elastica*, Fig. 55, G) of Fam. Moraceae, *Rhizophora mucronata* (Fam. Rhizophoraceae), *Capparis sepiaria* (Fam. Capparidaceae), *Cocculus villosus* (Fam. Menispermaceae), *Ecetinos achinthes-mucronata* (Fam. Apocynaceae), *Bupleurum mucronatum* (Fam. Umbelliferae), etc.

Tendrillar, when the apex is modified into a tendril, as in glory lily (*Gloriosa superba*, Fig. 55, H) of Fam. Liliaceae.

Cirrrose, when the apex ends in a fine thread-like structure, as in banana (*Musa paradisiaca* var. *sapientum*, Fig. 55, I) of Fam. Musaceae.

Truncate, when the apex appears to be abruptly cut across, as in *Paris polyphylla* (Fam. Liliaceae), *Indigofera linifolia* of S.F. Papilionaceae (Fam. Leguminosae), some palms, etc.

MARGIN OF LAMINA (Fig. 56)

The margin of the lamina may be :

Entire, when the margin is completely even and not at all cut or segmented, as in banyan (*Ficus benghalensis*, Fig. 56, A) of Fam. Moraceae, guava (*Psidium guayava*) of Fam. Myrtaceae, etc.

Repand, when the margin is entire but wavy, as in *Polyalthia longifolia* (Fig. 56, B) of Fam. Anonaceae.

Serrate, when the margin is indented like the teeth of a saw and these are directed towards the apex, as in rose (*Rosa centifolia*) of Fam. Rosaceae, China rose (*Hibiscus rosa-sinensis*, Fig. 56, C) of Fam. Malvaceae, margosa (*Melia azadirachta*) of Fam. Meliaceae, etc.

Dentate or toothed, when the teeth are prominent and directed outwards at right angles to the margins of the lamina, as in red water lily (*Nymphaea rubra*, Fig. 56, D) of Fam. Nymphaeaceae, *Aloe perfoliata* (Fam. Liliaceae), etc.

Crenate, when the teeth are more or less blunt and rounded, as in *Bryophyllum calycinum* (Fig. 33, A) of Fam. Crassulaceae, Indian pennywort (*Hydrocotyle asiatica*, Fig. 56, E) of Fam. Umbelliferae, etc.



FIG. 56. MARGIN OF LAMINA

A, Entire ; B, Repand ; C, Serrate ; D, Dentate ; E, Crenate ; F, Spiny.

Spiny, when the margin is provided with a number of spiny processes, as in Mexican poppy (*Argemone mexicana*, Fig. 56, F) of Fam. Papaveraceae, *Solanum xanthocarpum* (Fam. Solanaceae), barberry (*Berberis vulgaris*) and *Mahonia mysorensis* of Fam. Berberidaceae, etc.

Besides these types of margin, the primary indentations may bear secondary processes and give rise to the types like **bi-dentate**, **bi-serrate**, **bi-crenate**, and so on.

BASE OF LAMINA (Fig. 57)

Auriculate, when in some sessile leaves the leaf-base becomes winged, i.e., forms two lobes, which partially surround the stem, as in *Calotropis procera* (Figs. 57, A & 69, C) of Fam. Asclepiadaceae, Mexican poppy (*Argemone mexicana*) of Fam. Papa-

veraceae, *Sonchus oleraceus* (Fam. Compositae), *Conscora decussata* (Fam. Gentianaceae), etc.

Perfoliate, when the lobes at the base of a sessile leaf become fused together so as to surround the stem completely, as in *Aloe perfoliata* (Fam. Liliaceae), *Conscora perfoliata* (Fig. 57, B) of Fam. Gentianaceae, etc. In such a case, the stem appears to pass through the lamina.

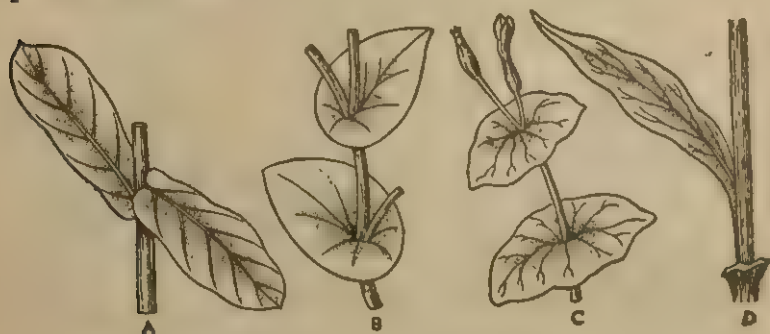


FIG. 57. BASE OF LAMINA

A, Auriculate ; B, Perfoliate ; C, Connate ; D, Decurrent.

Connate, when the bases of two opposite sessile leaves are completely fused together, as in *Swertia chirata* and *Canscora diffusa* (Fig. 57, C) of Fam. Gentianaceae, soapwort (*Saponaria vaccaria*) of Fam. Caryophyllaceae, etc.

Decurrent, when the leaf-base is winged and fused with the stem for some distance, as in *Sphaeranthus indicus* (Fig. 57, D) and *Laggera alata* of Fam. Compositae.

SURFACE OF LAMINA

The surface of the lamina may be :

Glabrous, when the surface of the lamina is smooth and free from hairs, as in pink (*Dianthus chinensis*) of Fam. Caryophyllaceae, *Pongamia glabra* and liquorice (*Glycyrrhiza glabra*) of S.F. Papilionaceae (Fam. Leguminosae).

Glaucous, when the surface has a coating of wax and appears to be bluish green and shiny, as in cabbage (*Brassica oleracea*) of Fam. Cruciferae, *Solanum glaucum* (Fam. Solanaceae), etc.

Viscid, when the surface is covered with a sugary exudation, as in *Polanisia icosandra*=*cleome viscosa* (Fam. Capparidaceae).

Glutinous, when the surface is covered with a sticky exudation, as in tobacco (*Nicotiana tabacum*) of Fam. Solanaceae.

Spinose, when the surface is covered with spines, as in brinjal (*Solanum melongena*) and *Solanum xanthocarpum* of Fam. Solanaceae.

Rugose, when the surface is wrinkled, as in *Rubus rugosus* (Fam. Rosaceae).

Hairy, when the surface is covered with hairs.

A hairy surface may be : (a) **pilose**, when covered with small, soft and scattered hairs, as in *Escholtzia pilosa* (Fam. Labiatae) ; (b) **hirsute**, if with long scattered hairs, as in *Ipomoea pes-tigridis* (Fam. Convolvulaceae) ; (c) **hispid**, with stiff scattered hairs, as in *Ficus hispida* (Fam. Moraceae), *Acalypha hispida* (Fam. Euphorbiaceae), etc. ; (d) **downy** or **pubescent**, if closely covered with short soft hairs, as *sāl* (*Shorea robusta*) of Fam. Dipterocarpaceae, *Abutilon indicum* (Fam. Malvaceae), bottle gourd (*Lagenaria vulgaris*) of Fam. Cucurbitaceae, etc. ; (e) **tomentose** or **cottony**, if with similar but rather dense and interwoven hairs, as in *Calotropis procera* (Fam. Asclepiadaceae), *Tinospora tomentosa* (Fam. Menispermaceae), *Guazuma tomentosa* (Fam. Sterculiaceae), etc. ; (f) **wooly**, if with long and interwoven hairs like wool, as in *Solanum verbascifolium* (Fam. Solanaceae).

TEXTURE OF LAMINA

The texture of the lamina may be :

Succulent, when the lamina is fleshy and more or less brittle, as in *Bryophyllum calycinum* and *Kalanchoe spathulata* of Fam. Crassulaceae, *Aloe indica* (Fam. Liliaceae), etc.

Coriaceous, when the lamina is tough and leathery, as in India rubber (*Ficus elastica*) of Fam. Moraceae, *Anthocephalus cadamba* (Fam. Rubiaceae), *Magnolia grandiflora* (Fam. Magnoliaceae), *Mimusops elengi* (Fam. Zapotaceae), *Calophyllum inophyllum* (Fam. Guttiferae), *Vanilla planifolia* and *Vanda roxburghii* of Fam. Orchidaceae, etc.

Membraneous, when the lamina is thin and easily flexible, as in rose (*Rosa centifolia*) of Fam. Rosaceae, *Zeuxine sulcata* (Fam. Orchidaceae), etc.

Glandular or **gland-dotted**, when the lamina is dotted with pellucid glands filled with essential oil, as in orange (*Citrus sinensis*), lemon (*Citrus limon*) and other plants of Fam. Rutaceae, custard apple (*Anona squamosa*) and other plants of Fam. Anonaceae, etc.

VENATION OF LAMINA (Fig. 58)

The blade of the lamina is always characterized by the presence of **veins** or **nerves**, which are more or less prominent on its lower surface. These veins branch out in various ways into gradually smaller branches, which finally run together, thus giving the lamina its characteristic venation. The mode or manner in which the veins are distributed in the lamina is known as **venation**. In many cases, however, there is only one prominent vein which runs through the middle of the lamina from its base to the apex; this principal vein is known as the **midrib**. The ultimate branches, by means of which the anastomoses between the veins are brought about, are known as **veinlets**.

The veins not only preserve the shape and flatness of the lamina, but also form its supporting framework on which the softer parts are fixed. These are the channels through which raw food materials and elaborated foods are carried in and out of the lamina.

There are two principal types of venation in the lamina of angiospermic plants*—**reticulate** and **parallel (striate)**. The former type may be taken as characteristic of the dicotyledons and the latter, of the monocotyledons. But reticulate venation is found as an exception in some of the monocotyledons, such as common arum (*Colocasia antiquorum*) of Fam. Araceae, *Dioscorea alata* (Fam. Dioscoreaceae), *Smilax macrophylla* (Fam. Liliaceae), etc. Similarly, parallel

*It is interesting to note that several conifers are univeined. A special type of venation, known as **dichotomous venation**, is rather common among ferns like *Adiantum*, *Marsilea*, etc., and the gymnosperm, *Ginkgo biloba*.

venation may also be found among some dicotyledons, like *Calophyllum inophyllum*, *Garcinia cowa*, and some other plants of Fam. Guttiferae.

I. RETICULATE VENATION

In reticulate venation either the midrib or the prominent veins branch repeatedly until most of the veinlets run together forming a complicated, irregular and complete network. The reticulate venation may be of the following two types.

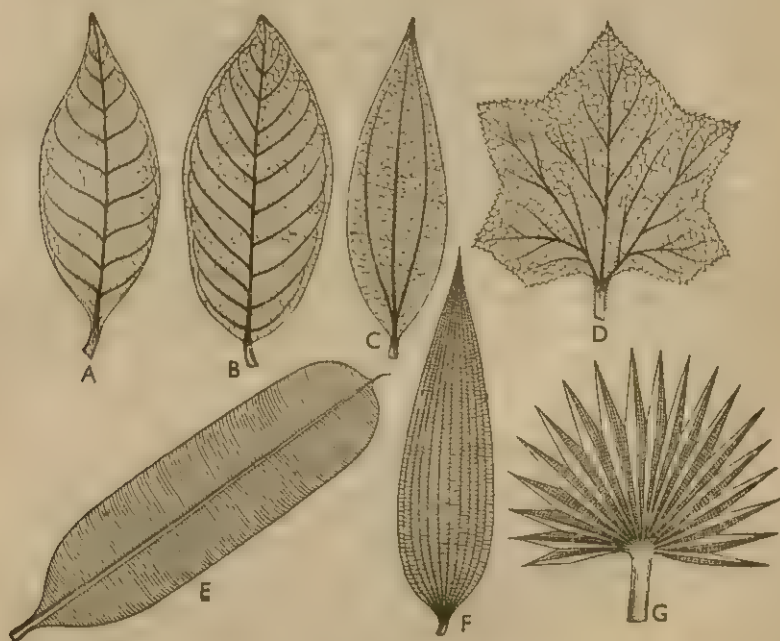


FIG. 58. VENATION

A, Reticulate unicostate ; B, Sub-marginal ; C, Reticulate multicostate (convergent) ; D, Reticulate multicostate (divergent) ; E, Parallel unicostate ; F, Parallel multicostate (convergent) ; G, Parallel multicostate (divergent).

Unicostate or pinnate. In this case there is a midrib, from which prominent veins branch out resembling the pinnae of a feather, and these ultimately anastomose by much-branched veinlets forming an irregular network, as in mango (*Mangifera*

indica, Fig. 58, A) of Fam. Anacardiaceae, jack (*Artocarpus integra*=*A. integrifolia*) of Fam. Moraceae, etc.

Occasionally, this type of venation give rise to a peculiar one, known as **sub-marginal venation**, in which some of the veins run parallel to the margins of the lamina, while others form the complicated network, as in guava (*Psidium guayava*, Fig. 58, B), rose-apple (*Eugenia jambos*), and some other plants of Fam. Myrtaceae.

Multicostate or palmate. In this case, there arise, instead of a single main vein, a number of large, prominent veins from the base of the lamina. It may be : (i) **convergent**, i.e., when the prominent veins arising from the base meet or appear to meet at the apex, as in cinnamon (*Cinnamomum tamala*, Fig. 58, C) of Fam. Lauraceae, jujube (*Zizyphus jujuba*) of Fam. Rhamnaceae, clearing nut (*Strychnos potatorum*) and *S. nuxvomica* of Fam. Loganiaceae, etc., and (ii) **divergent**, i.e., when the prominent veins arising from the base, instead of meeting at the apex, go further away from it in all directions, as in gourd (*Cucurbita maxima*, Fig. 58, D) and other plants belonging to Fam. Cucurbitaceae, China rose (*Hibiscus rosa-sinensis*), cotton (*Gossypium herbaceum*) and other plants of Fam. Malvaceae, *Sterculia foetida* and other plants of Fam. Sterculiaceae, *Grewia asiatica* (Fam. Tiliaceae), papaw (*Carica papaya*) of Fam. Caricaceae, etc.

II. PARALLEL OR STRIATE VENATION

In the parallel or striate venation, the principal veins run more or less parallel to one another, either from the base to the apex of the lamina, or at right angles to the midrib. These veins ultimately anastomose by short, straight and unbranched veinlets, but do not form any network. The parallel or striate venation, like the reticulate one, may also be *unicostate* and *multicostate*.

Unicostate or pinnate. In this case, there is a conspicuous midrib, from which many prominent veins not only develop and run parallel to one another at right angles to it, but also ultimately anastomose, as in banana (*Musa paradisiaca* var. *sapientum*, Fig. 58, E) of Fam. Musaceae, Indian shot (*Canna indica*) of Fam. Cannaceae, etc.

Multicostate or palmate. In this case, there arise, instead of a single main vein, a number of veins from the base of the lamina, and these run more or less parallel to one another. Like the reticulate multicostate venation, it may be : (i) **convergent**, as in grasses and bamboo (*Bambusa arundinacea*, Fig. 58, G) of Fam. Gramineae, and (ii) **divergent**, as in palmyra palm (*Borassus flabellifer*, Fig. 58, H) of Fam. Palmae.

MODIFICATIONS OF LAMINA

For performing diverse functions, the lamina may be modified, either wholly or in part. A brief account of such modifications is given in the following lines.

Leaf-tendrils. The lamina in some plants may be either wholly or partly modified into tendrils. Thus, in wild pea (*Lathyrus aphaca*, Fig. 59, A) of S.F. Papilionaceae (Fam. Leguminosae) the whole lamina, in *Naravelia zeylanica* (Fam. Ranunculaceae) and pea (*Pisum sativum*), Fig. 52, A) of S.F. Papilionaceae (Fam. Leguminosae) the terminal leaflet and leaflets respectively, in glory lily (*Gloriosa superba*, 59, B) of Fam. Liliaceae the apex, and in pitcher plant (*Nepenthes khasiana*) of Fam. Nepenthaceae, according to some authors, the midrib, are transformed into tendrils.

Spines. These are sharp-pointed structures. Morphologically, a spine may be a part, or the whole of the lamina modified. Primarily, these spines are developed as a means of defence for

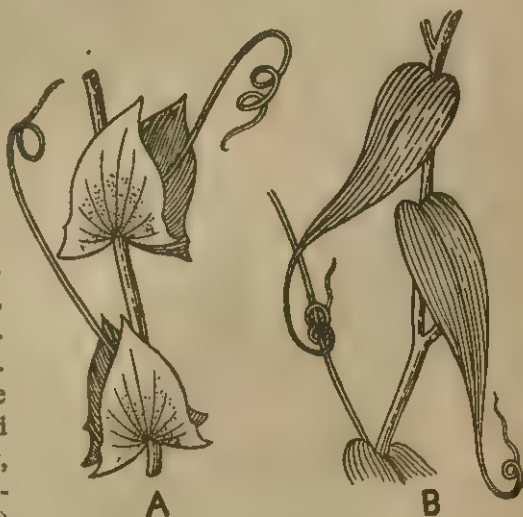


FIG. 59. LEAF-TENDRILS
A, of *Lathyrus* ; B, of *Gloriosa*.

protecting plants against the ravages of grazing animals. In extreme cases, however, as in plants growing in deserts and similar environments, these are developed both as a means of protection as well as that of reducing the transpiring surface. In the leaves of barberry (*Berberis aristata*) of Fam. Berberidaceae, all intermediate forms, between ordinary foliage leaf and its extreme modification into a spine, are very clearly seen. In prickly pear (*Opuntia dillenii*, Fig. 79, A) of Fam. Cactaceae and similar other cacti, *Asparagus racemosus* (Fig. 79, D) of Fam. Liliaceae, etc., the leaves are completely metamorphosed into spines, so much so, that the main leaf and the leaves of axillary buds appear as cluster of spines on short shoots, borne on the more or less flattened stem. Their morphological nature is determined by their position, which is always nodal, and sometimes by buds borne in their axils. In several species of *Citrus* (Fam. Rutaceae), the first leaf or first pairs of leaves of axillary buds become spiny. The apex of the lamina in *Jacquinia ruscifolia* (Fig. 80, F) of Fam. Theophrastaceae, date palm (*Phoenix sylvestris*, Fig. 77, H) of Fam. Palmae, etc.; margins in Mexican poppy

(*Argemone mexicana*, Fig. 80, E) of Fam. Papaveraceae, *Solanum xanthocarpum* (Fam. Solanaceae), etc.; the apex as well as the margins in *Agave cantula* (Fam. Amaryllidaceae), *Aloe indica* (Fam. Liliaceae), pineapple (*Ananasa sativa*) of Fam. Boromeliaceae, etc.; are transformed into spines. Sometimes in a compound leaf, some of the leaflets become modified into spines, as in *Parkinsonia aculeata* of S.F. Caesalpineae (Fam. Leguminosae).

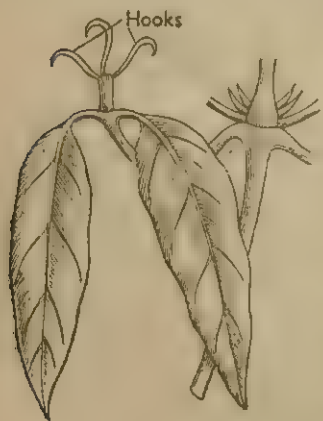


FIG. 60. Hooks

Hooks. In *Bignonia unguis-cati* (Fig. 60) of Fam. Bignoniaceae, three terminal leaflets become modified into very sharp and strong hooks. These hooks cling to the bark of trees and thus help the plant to climb up.

Root-like structures. In some water plants, such as water milfoil (*Myriophyllum indicum*) of Fam. Haloragidaceae,

Salvinia (a pteridophyte), etc., the submerged leaves are modified into slender root-like structures for absorption of water, and are frequently mistaken as such. Such plants do not possess any true root at all.

Pitcher. In the pitcher plant (*Nepenthes* sp., Fig. 14, A) of Fam. Nepenthaceae, the leaf is modified into a pitcher. Just below the pitcher there is a slender stalk, which coils like a tendril, and after that there is a flattened leafy body. The mouth of the pitcher is provided on one side with a small lid-like structure. The function of the pitcher is to capture insects in order to get nitrogenous supply from their bodies. There has been a considerable debate regarding the morphology of the leaf of the pitcher plant.*

Another peculiar modification of leaf into a kind of pitcher is illustrated by *Dischidia rafflesiana*. (Fam. Asclepiadaceae, Fig. 61), a common epiphytic climber of Assam. The pitcher is not insectivorous in nature like that of *Nepenthes*. Each pitcher has an apical opening (but without any lid) and becomes filled up with water usually after a shower.

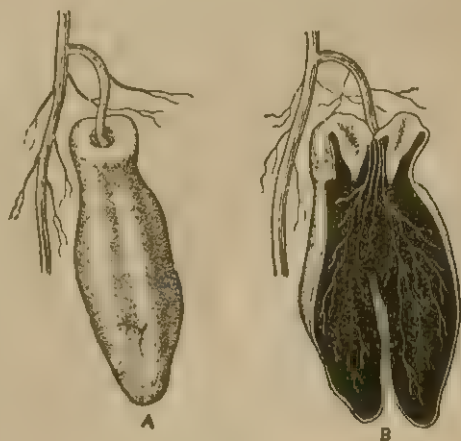


FIG. 61. PITCHER OF *Dischidia*
A, an entire pitcher ; B, the same split lengthwise.

The nodes, from which the pitchers develop, also give rise to

*The views regarding the morphology of the leaf of the pitcher plant may be very briefly summarised as follows :

(1) The apex of the lamina is modified into a pitcher. (2) The midrib of the lamina prolongs, and it is modified into a pitcher. (3) The whole leaf is modified. The petiole is winged for some distance from the base, and then becomes a tendril and ends in a pitcher furnished with a lid (*Green*). (4) The lamina is modified into pitcher (with a lid) ; the laminar portion is the modified leaf-base ; the tendril is the modified petiole (*Goebel*). (5) The leaf-base is quite normal. The petiole is modified and it consists of three

much-branched rootlets, which enter into the cavity and absorb water and humus already collected therein.

Bladder. In bladderwort (*Utricularia stellaris*, Fig. 14, B) of Fam. Lentibulariaceae, a rootless herb, which is commonly found in our old tanks, the submerged leaves are much segmented. Some of these segments are modified to form bladder-like structures. These bladders are devices for entrapping insects to obtain nitrogen from their bodies.

SIMPLE AND COMPOUND LEAVES

The lamina either consists of a single piece with entire or indentated margins, or is completely divided and separated into distinct individual parts (**leaflets**). Thus, two types of leaves can be recognized : (a) **simple** (Fig. 62, A & C), and (b) **compound**. A simple leaf is one, in which the lamina presents a single appearance whether lobed or undivided. On the other hand, in a compound leaf the lamina is completely dissected into separate leaflets, which are articulated, either along a central axis, called **rachis**, or around a common point at the end of the rachis. According to the nature of arrangement of leaflets*, a compound leaf is either of a pinnate or of a palmate type. A leaf is said to be **pinnately compound** (Fig. 62, B), when the leaflets borne by the rachis are arranged on its two sides, like the pinnae of a feather. In this case, it is obvious that the rachis really corresponds to the midrib of a simple leaf with pinnate venation. But, in case of a **palmately compound** leaf (Fig. 62, D), the rachis is entirely suppressed,

parts : the laminar part, the tendrillar part and the pitcher ; the lid of the pitcher is the modified lamina proper. There is a distinct articulation at the base of the lid with the mouth of the pitcher at the point of attachment, which proves that the lid is a modified unifoliate compound leaf (*Banerjee*).

*The point of attachment of a leaflet to the rachis is known as **articulation**. Formerly, the presence of articulation was regarded as one of the criteria of a compound leaf, but recently, articulations have been noted in case of simple leaves as well, and as such, the older view has been discarded.

so that the leaflets seem to arise from a common point at the end of the rachis.



FIG. 62. SIMPLE AND COMPOUND LEAVES

A, Simple (Pinnate) ; B, Pinnately compound ; C, Simple (Palmate) ; D, Palmately compound.

A compound leaf is often mistaken for a branch with simple leaves, but the following distinguishing features will obviate the difficulty.

(1) A compound leaf never bears a terminal bud, whereas, a leafy branch always does so. (2) A compound leaf always bears a bud in the axil of its rachis, but itself does not arise in the axil of another leaf ; whereas, a branch never bears a bud in its axil, but itself is axillary in position and arises from an axillary bud. (3) The leaflets of a compound leaf have no axillary buds, whereas, the simple leaves on the branch bear such buds in their axils. (4) The rachis of a compound leaf never possesses any node or internode, whereas, a branch invariably does so. (5) A compound leaf falls off as a whole leaving a scar on the stem, but a branch never falls off as such.

Incision of the lamina (Figs. 63 & 64)

The lamina of a simple leaf, whether pinnately or palmately veined, is often incised or lobed.

In the pinnately veined leaf the incisions take place in between the veins, and extend inwardly towards the midrib from the margins. According to the extent of these incisions, several types of lamina are recognised : (a) **pinnatifid**, if the incisions extend less than half-way down towards the midrib, as in chrysanthemum (*Chrysanthemum coronarium*, Fig. 63, A) of Fam. Compositae, opium poppy (*Papaver somniferum*) of Fam. Papaveraceae, etc. ; (b) **pinnatipartite**, if the incisions are more than half-way down towards the midrib, as in Mexican poppy (*Arge-*

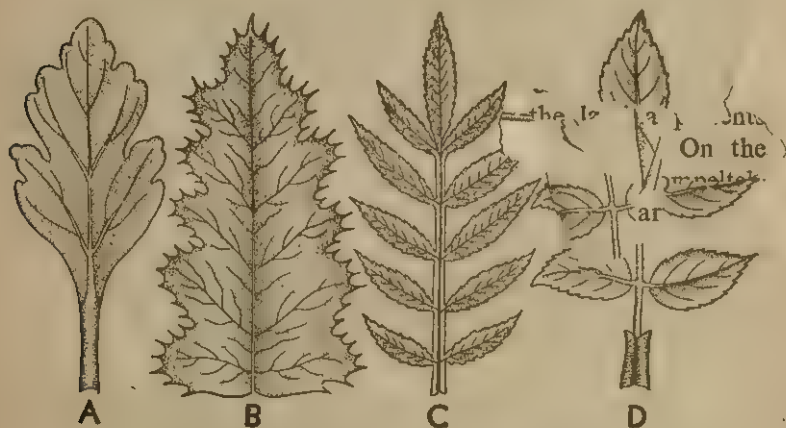


FIG. 63. INCISIONS OF LAMINA (Pinnate type)

A, Pinnatifid ; B, Pinnatipartite ; C, Pinnatisect ; D, Pinnate compound.

mone mexicana, Fig. 63, B) of Fam. Papaveraceae, water chestnut (*Trapa bispinosa*) of Fam. Onagraceae, mustard (*Brassica nigra*) and radish (*Raphanus sativus*) of Fam. Cruciferae, etc. ; (c) **pinnatisect**, if the incisions almost reach the midrib, as in marigold (*Tagetes patula*, Fig. 63, C) of Fam. Compositae, *Ipomoea quamoclit* (Fam. Convolvulaceae), coconut palm (*Cocos nucifera*) and date palm (*Phoenix sylvestris*) of Fam. Palmae etc; (d) **pinnate compound**, when the incisions reach the midrib, so that the segments are quite separated forming leaflets, as in rose (*Rosa centifolia*, Fig. 63, D) of Fam. Rosaceae, *Murraya exotica* (Fam. Rutaceae), etc.

In the palmately veined leaf the incisions proceed from the margins towards the base of the lamina. As in the preceding

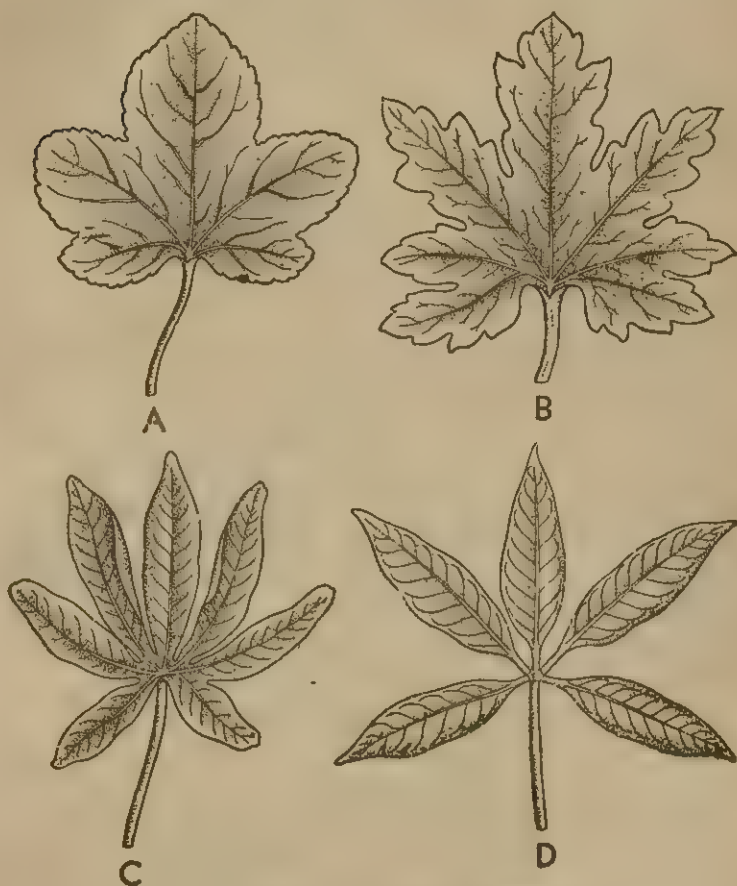


FIG. 64. INCISIONS OF LAMINA (Palmate type)

A, Palmatifid ; B, Palmatipartite ; C, Palmatisect ; D, Palmate compound.

cases, the incisions give rise to several types of lamina : (a) **palmatifid**, as in lady's finger (*Hibiscus esculentus*) and cotton (*Gossypium herbaceum*, Fig. 64, A) of Fam. Malvaceae, papaw (*Carica papaya*) of Fam. Caricaceae, *Jatropha curcas* (Fam. Euphorbiaceae), etc. ; (b) **palmatipartite**, as in bitter melon (*Momordica charantia*), of Fam. Cucurbitaceae, castor (*Ricinus com-*

munis, Fig. 64, B) of Fam. Euphorbiaceae, etc. ; (c) **palmaisect**, as in morning glory (*Ipomoea pulchella*, Fig. 64, C) and *I. paniculata* of Fam. Convolvulaceae ; (d) **palmate compound**, as in silk cotton tree (*Salmaalial malabarica*=*Bombax malabaricum*, Fig. 64, D) of Fam. Bombacaceae.

As mentioned before, there are two types of compound leaf : pinnate and palmate.

PINNATE COMPOUND LEAVES (Fig. 65)

A pinnate compound leaf is one in which the leaflets (**pinnae**) are arranged in pairs along the two sides of a rachis, like the plumes of a feather. There are several types of pinnate compound leaf as follows.

Unipinnate, when the rachis bears the leaflets directly ; it may, in its turn, be of the following types.

Imparipinnate. if the rachis is terminated by an unpaired or odd leaflet, as in rose (*Rosa centifolia*, Fig. 65, A) of Fam. Rosaceae, *Clitoria ternatea* of S.F. Papilionaceae (Fam. Leguminosae), *Murraya exotica* (Fam. Rutaceae), etc.

Paripinnate, if the rachis is terminated by an even number of leaflets, as in tamarind (*Tamarindus indica*, Fig. 65, B), gold mohur (*Delonix regia*=*Poinciana regia*), *Cassia fistula*, and most plants of S.F. Caesalpinieae (Fam. Leguminosae).

Pinnately trifoliate, if the number of leaflets be three, as in *Trigonella foenambellus*, *Crotalaria trifoliatum* and *C. incana* of S.F. Papilionaceae (Fam. Leguminosae).

Interruptedly pinnate, if pairs of large leaflets alternate with pairs of small leaflets, as in potato (*Solanum tuberosum*, Fig. 65, C) of Fam. Solanaceae.

Cirrhiferously pinnate, if the terminal leaflets are converted into tendrils, as in pea (*Pisum sativum*, Fig. 65, D) of S.F. Papilionaceae (Fam. Leguminosae).

Unipinnate compound leaves may also be called **unijugate**, if there be only one pair of leaflets, as in beans, **bijugate**, if there be two pairs of leaflets, as in ground nut (*Arachis hypogaea*) of S.F. Papilionaceae (Fam. Leguminosae), **trijugate**, if there be three pairs of leaflets as in *Rhus wallichii* (Fam. Anacardi-

ceae), and **pentajugate**, if there be five pairs of leaflets, as in *Odina wodier* (Fam. Anacardiaceae), etc.



FIG. 65. PINNATE COMPOUND LEAVES.

A, Imparipinnate of rose ; B, Paripinnate of tamarind ; C, Interruptedly pinnate of potato ; D, Cirrhiferously pinnate of pea ; E, Bipinnate, of *Acacia* ; F, Tripinnate of *Moringa* ; G, Decompose of anise.

Bipinnate, when the leaflets of a pinnate leaf are again pinnately incised into distinctly smaller segments (**pinnules**), as in gum tree (*Acacia arabica*, Fig. 65, E) and sensitive plant (*Mimosa pudica*) of S.F. Mimosae, peacock flower (*Caesalpinia pulcherrima*) of S.F. Caesalpinieae, all belonging to Fam. Leguminosae.

Tripinnate, when the pinnules of a bipinnate leaf are again pinnately incised, as in horse radish (*Moringa pterygosperma*, Fig. 65, F) of Fam. Moringaceae, *Melia azadirachta* (Fam. Meliaceae), etc.

Decomposed, when the leaflet is several times pinnately incised, as in anise (*Foeniculum vulgare*, Fig. 65, G), carrot (*Daucus carota*), *Peucedanum sowa*, and most of the plants of Fam. Umbelliferae.

PALMATE COMPOUND LEAVES (Fig. 66)

A palmate compound leaf is one in which the leaflets are arranged at a common point at the end of the rachis. There are several types of palmate compound leaf as follows.

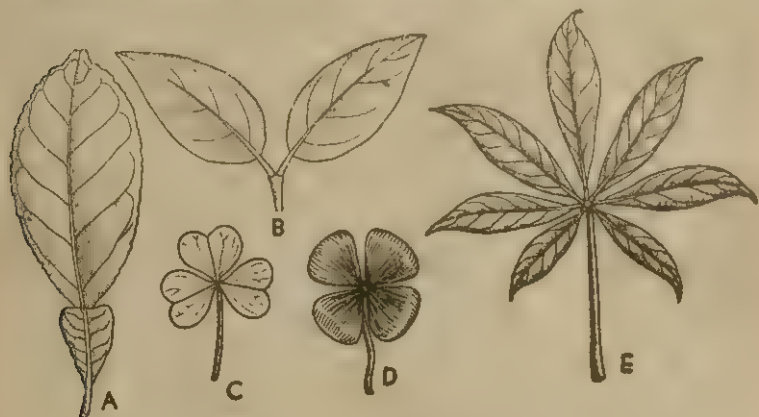


FIG. 66. PALMATE COMPOUND LEAVES

A, Unifoliate of lemon ; B, Bifoliate of *Hardwickia* ; C, Trifoliate of *Oxalis* ; D, Quadrifoliate of *Marsilea* ; E, Digitate of *Salmalia*.

Unifoliate,* when a single leaflet is articulated at the end of the rachis, as in lemon (*Citrus limon*, Fig. 66, A), orange (*Citrus sinensis*) and shaddock (*Citrus decumana*) of Fam. Rutaceae. According to some authors, the lid of the pitcher in *Nepenthes* sp. (Fam. Nepenthaceae) illustrates a unifoliate compound leaf.

Bifoliate or **binnate**, when two leaflets are articulated at the end of the rachis, as in *Balanites roxburghii* (Fam. Simarubae), *Hardwickia pinnata* (Fig. 66, B) and *Inga dulcis* of S.F. Papilionaceae (Fam. Leguminosae), *Bignonia grandiflora* (Fam. Bignoniaceae), etc.

*Recent workers suggest that the leaf of *Citrus* sp. is a simple one, and hence, the term 'unifoliate compound leaf' has been discarded.

Trifoliate or **ternate**, when three leaflets are articulated at the end of the rachis as in wood sorrel (*Oxalis corniculata*, Fig. 66, C) of Fam. Oxalidaceae, wood apple* (*Aegle marmelos*) of Fam. Rutaceae, *Vitex negundo* (Fam. Verbenaceae), etc.

Quadrifoliate or **quadrinate**, when four leaflets are articulated at the end of the rachis, as in *Marsilea quadrifolia* (a pteridophyte, Fig. 66, D).

Digitate, when more than four leaflets are articulated at the end of the rachis, as in silk cotton tree (*Salvia malabarica* = *Bombax malabaricum*, Fig. 66, E) of Fam. Bombacaceae, *Sterculia foetida* (Fam. Sterculiaceae), *Dioscorea pentaphylla* (Fam. Dioscoreaceae), *Alstonia scholaris* (Fam. Apocynaceae), tapioca (*Manihot utilissima*) of Fam. Euphorbiaceae, etc.

FUNCTIONS OF LEAVES

I. Normal functions. The normal functions of leaves are : (a) photosynthesis (i.e., manufacture of carbohydrate food), (b) respiration, and (c) transpiration (i.e., giving off of excess water in the vapour state).

II. Special functions. Besides the normal functions, the leaf often undergoes partial or total modification as an adaptation to various other requirements,—mechanical and physiological.

(a) Special mechanical functions

Protection. Leaves may be wholly, (as in prickly pear) or partly, (as in date, pine apple, etc.) modified into spines for protection against herbivorous animals.

Climbing. Leaves may be wholly, (as in wild pea), or partly, (as in glory lily, pea, etc.) modified into tendrils for climbing over supports. Sometimes they are modified into hook-like structures, also meant for climbing, as in *Bignonia unguis-cati* (Fam. Bignoniaceae).

(b) Special physiological functions

Storage of food and water. Leaves often store water or food for the future use of the plant. Such leaves generally become fleshy or succulent. Thus, the leaves of *Aloe indica*

*The real morphological nature is doubtful.

(Fam. Liliaceae), *Portulaca oleracea* (Fam. Portulacaceae), *Basella rubra*, sea blight (*Suaeda maritima*) and salt-wort (*Salsola kali*) of Fam. Chenopodiaceae, *Kalanchoe spathulata* and *Bryophyllum calycinum* of Fam. Crassulaceae, etc., are fleshy on account of storage of either water and mucilage or food. As a matter of fact, the succulent leaf very often indicates the xerophytic nature of the plant. Fleshy leaves in many cases serve as an additional organ of vegetative reproduction. The leaves of *Bryophyllum*, *Kalanchoe*, and *Begonia picta* (Fam. Begoniaceae), etc., develop adventitious buds, which give rise to new plants. In *Dischidia rafflesiana* the leaves are modified into pitcher-like structures for storing water as well as humus.

Absorption of water. Leaves of some water plants, (such



FIG. 67. LEAF-TIP PROPAGATION IN *Cramptosorus*

as water-milfoil, *Salvinia*, etc.), are highly modified into slender root-like structures for absorption of water.

Reproduction. Leaves may produce new plants vegetatively by means of epiphyllous buds, as in *Bryophyllum*, *Kalanchoe*,

Begonia, etc. Sometimes, apices of leaves on coming in contact with the soil strike root and form new plants, as in walking fern (*Cramptosorus rhizophyllus*, Fig. 67 and *Asplenium rhizophyllum*), maiden hair fern (*Adiantum* sp.), *Curculigo* sp. (Fam. Amaryllidaceae), etc.

Insect traps. The leaves of the insectivorous plants (Fig. 14) are modified into various kinds of traps for capturing insects in order to obtain nitrogenous food from their bodies, as in pitcher plant, bladderwort, etc.

ARRANGEMENT OF LEAVES

As described before, the leaves in the bud condition remain packed, rolled or folded on a very short axis. With the gradual elongation of the axis, these leaves unfold and become separated from one another. Their arrangement on the older stem then differs from that in the bud. Thus, two types of arrangement of leaves are distinguished, viz., (a) **prefoliation**, or the disposition of the leaves in the bud, and (b) **phyllotaxy**, or the arrangement of leaves on the stem or branches.

PREFOLIATION*

The manner in which the leaves are arranged in the bud can be considered under two heads, viz., (i) the manner in which the individual leaf (considered independently of others) remains bent, rolled, or folded in the bud (**ptyxis**, Fig. 68), and (ii) the relation amongst several leaves of the same bud taken collectively (**vernation**). As to each leaf considered separately, it comprises of two aspects : those in which the leaf remains bent or folded, and those in which it is rolled up.

(a) *Leaf bent or folded*

There are the following four principal types.

Reclinate or inflexed, when the upper part is half bent inwards towards the base of the lamina, as in loquat (*Eriobotrya japonica*) of Fam. Rosaceae.

*This term is also used as synonymous with 'vernation' by some authors.

Conduplicate, when the leaf is folded lengthwise along the midrib, so that the two halves of the blade remain face to face, as in rose (*Rosa centifolia*) of Fam. Rosaceae, *Magnolia grandiflora* (Fam. Magnoliaceae), etc. It is the most common type of arrangement in unicostate leaves.

Plicate, when the leaf is folded several times along its main veins like a closed fan as in palmyra palm (*Borassus flabellifer*) of Fam. Palmae, *Pogonia* sp. and *Geodorum* sp. of Fam. Orchidaceae, etc. It is the most common type of arrangement in multicostate divergent leaves.

Crumpled, when it is folded irregularly in all directions, as in the cabbage (*Brassica oleracea*) of Fam. Cruciferae.

(b) Leaf rolled

There are also four principal types as follows.

Circinate, when the leaf is rolled from the apex towards the base on its axis like the hairspring of a watch, as in ferns, *Cycas* (a gymnosperm), etc.

Convolute, when the leaf is rolled up in one direction from one margin to the other as in banana (*Musa paradisiaca* var.

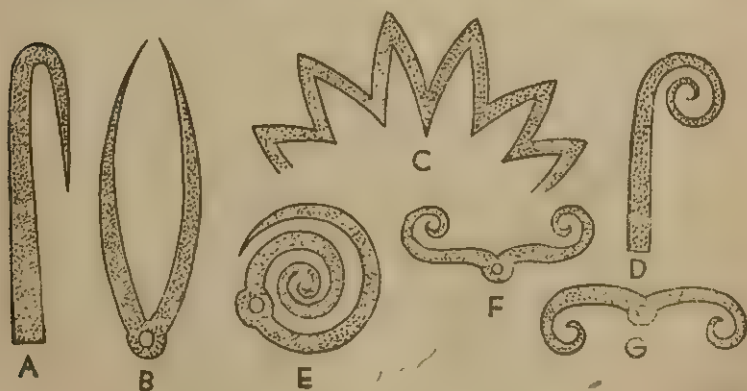


FIG. 68. PLYXIS (Diagrammatic)

A, Vertical section of a reclinute leaf ; B, t.s. of a conduplicate leaf ; C, t.s. of a plicate leaf ; D, v.s. of a circinate leaf ; E, t.s. of a convolute leaf ; F, t.s. of an involute leaf ; G, t.s. of a revolute leaf.

sapientum) of Fam. Musaceae, Indian shot (*Canna indica*) of Fam. Cannaceae, etc.

Involute, when both the margins of a leaf are rolled upwards towards the midrib, as in lotus (*Nelumbo nucifera*=*Nelumbium speciosum*) and water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae, jack (*Artocarpus integra*=*A. integrifolia*) and banyan (*Ficus benghalensis*) of Fam. Moraceae, etc.

Revolute, when both the margins of a leaf are rolled downwards towards the midrib, as in oleander (*Nerium odorum*) of Fam. Apocynaceae, *Polygonum* sp. (Fam. Polygonaceae), country almond (*Terminalia catappa*) of Fam. Combretaceae, etc.

When the relationship of several leaves (of the same bud) to one another is collectively considered, the following four types may be recognised.

Equitant, when both the margins of a conduplicate leaf enclose the next inner and opposite leaf in a regular order, as in blue flag (*Iris nepalensis*) and corn flag (*Gladiolus communis*) of Fam. Iridaceae.

Valvate, when the margins of leaves just touch one another but do not overlap.

Twisted, when the margins of the leaves are overlapped by one another in regular succession.

Imbricate, when the arrangement is such that one is completely external, one completely internal, and others are as in the twisted one.

In the last three types the component leaves remain flat or slightly convex. Similar terms are also used for the arrangement of the outer members of the floral buds under the collective name of **aestivation** or **prefloration**.

PHYLLOTAXY (Fig. 69)

The mode of arrangement of the adult leaves on the stem or the branch is known as **phyllotaxy**. The leaves are not arranged haphazardly on the stem, but in a definite plan and at regular intervals. The object of such arrangements is to cut down shading to a minimum, and to place the leaves in favourable positions to obtain the maximum amount of sunlight to carry on their functions successfully. Each plant has, as a rule, a particular type of arrangement, which is its inherent

characteristic feature. Three principal types of phyllotaxy are recognised. These are discussed below.

Alternate or scattered, when a single leaf develops at a node, as in China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, mango (*Mangifera indica*, Fig. 69, A) of Fam. Anacardiaceae, tobacco (*Nicotiana tabacum*) of Fam. Solanaceae, etc.

Opposite, when there are two leaves at each node and are placed one opposite the other. It is of two kinds :

(a) **Decussate**, when the opposite leaves at one node stand

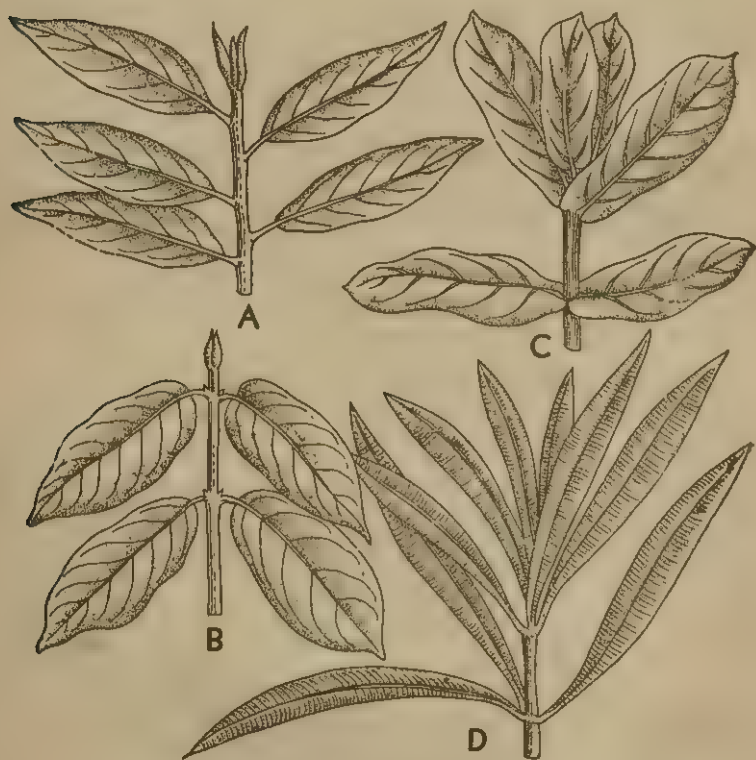


FIG. 69. PHYLLOTAXY

A, alternate of mango ; B, opposite superposed of *Hiptage* ; C, opposite decussate of *Calotropis* ; D, whorled of oleander.

at right angles to the pair above or below, thus forming four longitudinal rows of leaves round the stem, as in *Calotropis pro-*

cera (Fam. Asclepiadaceae, Fig. 69, C), *Ixora parviflora* (Fam. Rubiaceae), basil (*Ocimum sanctum*) of Fam. Labiatae, etc.

(b) **Superposed**, when the successive pairs of opposite leaves are placed one above the other, as in guava* (*Psidium guayava*) of Fam. Myrtaceae, *Aganosma caryophyllata* of Fam. Apocynaceae, *Hiptage madablota* (Fam. Malpighiaceae, Fig. 69, B), etc.

Whorled or verticillate, when more than two leaves arise at a node forming a verticel or whorl, as in oleander (*Nerium odoratum*, Fig. 69, D) of Fam. Apocynaceae.

The alternate phyllotaxy is also known as the **spiral phyllotaxy**. It is governed by certain laws : (1) leaves of a plant are not placed on one side of the stem but all round it ; (2) when imaginary straight lines are drawn vertically upwards and downwards on the stem through vertical rows of leaves, all the leaves on the plant will lie on them ; these imaginary vertical lines are known as **orthostichies** ; (3) the orthostichies are placed at an equal distance from one another ; (4) when the leaf-bases are joined together in succession, an imaginary continuous spiral, known as the **genetic spiral**, will be described ; (5) the distance between two successive leaves on the genetic spiral is known as the **divergence**, which subtends an angle at the centre of the stem, called the **angle of divergence** or **angular divergence**.

The angular divergence is denoted by the fraction a/b of 360° , where the numerator denotes the number of turns of a genetic spiral required to pass from one leaf to the next one vertically above it, and the denominator denotes either the number of leaves intercepted between the two such vertically situated leaves, omitting either the first or the last leaf, or the number of orthostichies.

According to the number of orthostichies, there are several kinds of spiral phyllotaxy, as described below.

Distichous or two-ranked (Fig. 70, A). In this case, there are two orthostichies, and one turn of the genetic spiral is required to pass from one leaf to the next one situated just vertically above it. It will be noticed that the third leaf is situated above the first, the fourth one above the second, so on. Distichous

*Guava sometimes exhibits decussate phyllotaxy also.

arrangement is denoted by the fraction $\frac{1}{2}$. Familiar examples are found in paddy (*Oryza sativa*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and other plants of Fam. Gramineae.

Angular divergence = $\frac{1}{2}$ of $360^\circ = 180^\circ$.

Tristichous or **three-ranked** (Fig. 70, B). In this case, there are three orthostichies, and one turn of the genetic spiral is required to pass from one leaf to next one situated just vertically above it. It will be noticed that the fourth leaf is situated above the first, the fifth one above the second, the sixth one above the third, and so on. Tristichous arrangement is denoted by the fraction $\frac{1}{3}$. The best example is sedge (*Cyperus rotundus*) of Fam. Cyperaceae.

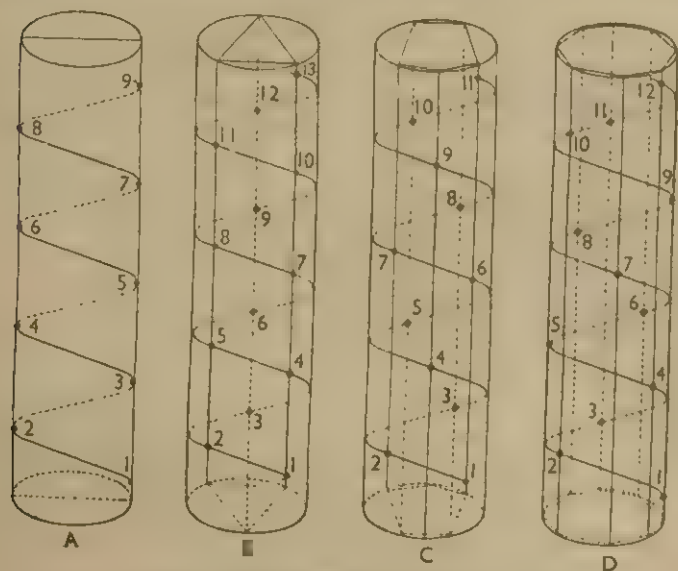
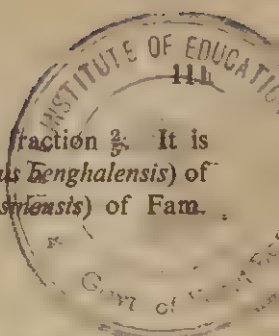


FIG. 70. SPIRAL PHYLLOTAXY (Diagrammatic)

A, Distichous ; B, Tristichous ; C, Pentastichous ; D, Octastichous.

Angular divergence = $\frac{1}{3}$ of $360^\circ = 120^\circ$.

Pentastichous or **five-ranked** (Fig. 70, C). In this case, there are five orthostichies, and two turns of the generic spiral are required to pass from one leaf to the next one situated just vertically above it. It will be found that the sixth leaf is above the first, the seventh one above the second, the eighth one above the third, and so on.



Pentastichous arrangement is denoted by the fraction $\frac{2}{5}$. It is very common and can be found in banyan (*Ficus Benghalensis*) of Fam. Moraceae, China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, etc.

Angular divergence = $\frac{2}{5}$ of $360^\circ = 144^\circ$.

The next type of arrangement is octastichous or eight-ranked one (Fig. 70, D) which is represented by the fraction $\frac{3}{8}$. In this type, there are eight orthostichies, and three turns of the genetic spiral are required to pass from one leaf to the next one situated

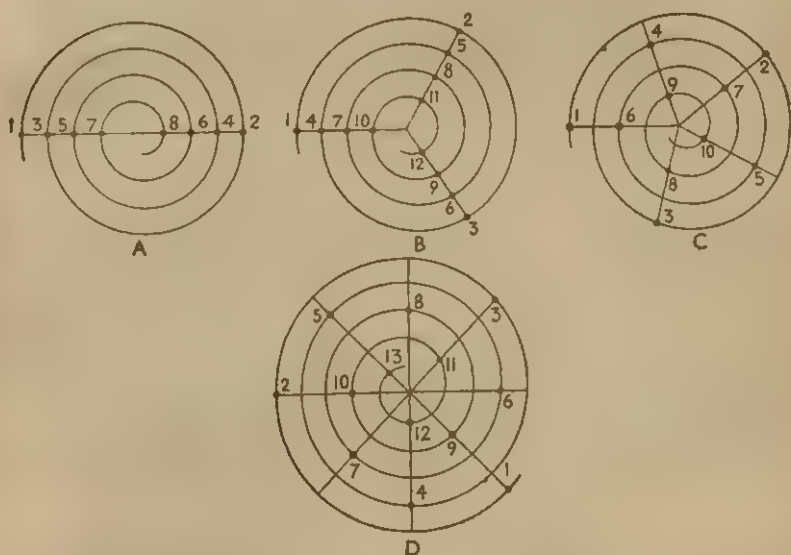


FIG. 71. SPIRAL PHYLLOTAXY (*Transverse projections*)

A, Distichous ; B, Tristichous ; C, Pentastichous ; D, Octastichous.

just vertically above it. It will be found that the ninth leaf is above the first, the tenth one above the second, and so on. Familiar examples are banana (*Musa paradisiaca* var. *sapientum*) of Fam. Musaceae, papaw (*Carica papaya*) of Fam. Caricaceae, *Thevetia peruviana* = *T. nerifolia* (Fam. Apocynaceae), etc.

Angular divergence = $\frac{3}{8}$ of $360^\circ = 135^\circ$.

Thus, it is found that the fractions are denoted by $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, etc. It is to be noted that each fraction, excepting the first two, is obtained by adding separately the numerators and denominators of the two preceding fractions. Hence, there is a mathematical relation in the arrangement of leaves with an automatically balanced symmetry. This is known as the **fibonacci series** in plants.

Phyllotaxy can also be determined by transverse projections (Fig. 71). When the spirally arranged leaves are very closely set, i.e., the divergences are very small, it is often very difficult to make out the orthostichies. In such cases, however, one finds well-marked lateral or diagonal stichies, known as **parastichies** (Fig. 72). Familiar examples are date palm (*Phoenix sylvestris*) of Fam. Palmae, male strobilus of *Cycas*, female cone of *Pinus*, etc.

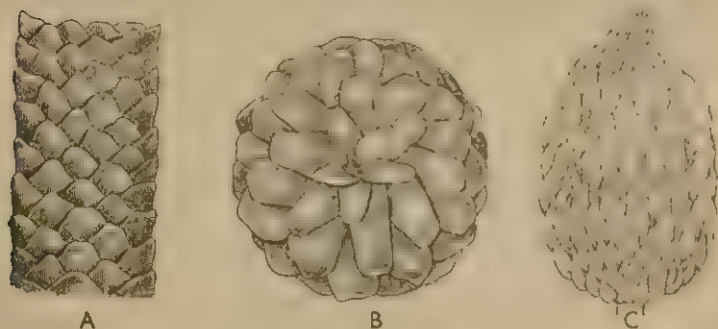


FIG. 72. PARASTICHIES

A, in date palm ; B, in female cone of *Pinus* ; C, in male cone of *Cycas*.

LEAF-MOSAIC (Fig. 73)

In the forests, dense jungles, bushes and even on walls and shady places, patches of light fall for a short duration only. The plants growing in these places often display a very beautiful arrangement of small and large leaves on the stem. The large leaves have gaps between them, and these are occupied by smaller ones, which twist and turn in such a manner that no space is left unoccupied. The result is a continuous green leafy surface

composed of various sizes and shapes of leaves. This is known as **leaf-mosaic**. It is common in wood sorrel (*Oxalis corniculata*) of Fam. Oxalidaceae, and garden nasturtium (*Tropaeolum majus*) of Fam. Tropaeolaceae, etc.

HETEROPHYLLY

A few plants bear foliage leaves of different forms on the same individual; this condition is known as **heterophylly**.

Heterophylly is chiefly found in many aquatic plants, such as water crowfoot (*Ranunculus aquatilis*) of Fam. Ranunculaceae, water chestnut (*Trapa bispinosa*) of Fam. Onagra-



FIG. 73. LEAF-MOSAIC IN *Tropaeolum*



FIG. 74. HETEROPHYLLY IN *Sagittaria sagittifolia*.

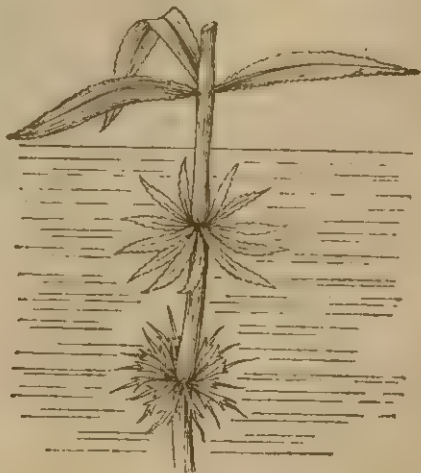


FIG. 75. HETIROPHYLLY IN *Limnophila*.

ceae, arrowhead (*Sagittaria sagittifolia*, Fig. 74) and water plantain (*Alisma plantago*) of Fam. Alismataceae, *Limnophila*

heterophylla (Fig. 75) of Fam. Scrophulariaceae, etc. In these plants there are two kinds of leaves, floating and submerged. The former are larger in size, undivided or lobed, while the latter are narrow or finely dissected. Heterophylly is sometimes found in land plants as well, as in coriander (*Coriandrum sativum*) of Fam. Umbelliferae, *Sterculia alata* and *Pterospermum acerifolium* of Fam. Sterculiaceae, *Ficus heterophylla* and *Artocarpus chaplasi* of Fam. Moraceae, *Leonurus sibiricus* (Fam. Libiatae), Indian buttercup (*Ranunculus sceleratus*) of Fam. Ranunculaceae, etc. Some marshy plants, like *Cardenthera triflora* (Fam. Acanthaceae), very frequently exhibit heterophylly. Such a condition is by no means confined to the angiosperms only, as it can be found in the pteridophytes (as in *Ceratopteris thalictroides* of Fam. Parkeriaceae, *Pteris ludens* and *Dymoglossum piloselloides* of Fam. Polypodiaceae) and in gymnosperms (as in *Ginkgo* of Fam. Ginkgoaceae), etc.

ECONOMIC IMPORTANCE OF LEAVES

Leaves mainly provide important sources of food, fibres and medicines. The green leaves of cabbage (*Brassica oleracea*) of Fam. Cruciferae, *Rumex vesicarius* (Fam. Polygonaceae), celery (*Apium graveolens*) of Fam. Umbelliferae, lettuce (*Lactuca sativa*) of Fam. Compositae, *Amaranthus viridis* (Fam. Amaranthaceae), spinach (*Spinacia oleracea*), *Basella rubra* (Fam. Basellaceae), and *Chenopodium album* (Fam. Chenopodiaceae), etc., are common vegetables. The fleshy underground leaves of onion, garlic, etc., are frequently used for cooking purposes. These leafy vegetables are very rich in their vitamin contents, and thus help in nutrition. The leaves of *Eragrostis cynosuroides* (Fam. Gramineae) are used by the Hindus in religious ceremonies. The juice of the leaves of *Eclipta alba*, *Widelia calendulacea* and *Calendula officinalis* of Fam. Compositae is used as a hair-tonic; that of the first-mentioned plant is also used in tattooing the skin. Many important fibres of commerce, like Manila hemp (*Musa textilis*) of Fam. Musaceae, sisal hemp (*Agave sisalana*) of Fam. Amaryllidaceae, and New Zealand hemp (*Phormium tenax*) of Fam. Liliaceae, are obtained from the leaves. These fibres are chiefly meant for making twine, rope, etc. Quite a good number of important drugs and narcotics are also obtained.

from the leaves. For example, the leaves of cocoa plant (*Theobroma cacao*) of Fam. Sterculiaceae yield cocaine, those of *Cannabis sativa* of Fam. Moraceae provide hemp, etc. ; tobacco is obtained from the leaves of *Nicotiana tabacum* (Fam. Solanaceae). Important drugs, like digitalin from *Digitalis purpurea* (Fam. Scrophulariaceae), stramonium from *Datura stramonium* (Fam. Solanaceae), belladonna and atropine from *Atropa belladonna* (Fam. Ranunculaceae), etc., are also leaf-products. Leaves of *Swertia chirata* (Fam. Gentianaceae), *Corchorus acutangularis* (Fam. Tiliaceae), *Eupatorium ayapana* (Fam. Compositae), *Adhatoda vasica* and *Andrographis paniculata* of Fam. Acanthaceae, *Vitis setosa* (Fam. Vitaceae), *Poederia foetida* (Fam. Rubiaceae), *Bacopa monnieri* (Fam. Scrophulariaceae), *Hydrocotyle asiatica* (Fam. Umbelliferae), *Ocimum sanctum* (Fam. Labiatae), etc., are extensively used in India as specific medicines. Leaves of *Phoenix paludosa* and *Nipa fruticans* of Fam. Palmae, *Typha angustata* (Fam. Typhaceae), etc., are used for thatching, and those of *Saccharum spontaneum* (Fam. Gramineae) are used as a substitute for straw-thatching. The universal beverage tea is obtained from the leaves of *Cammelia thea* of Fam. Cammeliaceae, cultivated extensively in India, Ceylon, China and Japan.

CHAPTER IV

HOMOLOGY, ANALOGY AND DEFENSIVE ORGANS

It has already been stated that roots, stems and leaves undergo modifications to carry on special functions. In order to understand these modifications, one must try to find out first what that modified organ really is, that is to say, what it corresponds to in the normal plant, whether to the root or to the shoot portion (stem, leaf, stipule, etc.), and secondly, why it has that particular form, and what end the modification serves.

Homology is the study of the organs as regards their resemblance to some morphological units in origin, development and position. **Analogy** is the study of the organs, which are adapted to the same physiological function, though they may be morphologically different.

HOMOLOGY OF CLIMBING ORGANS (TENDRILS)

(1) The tendrils of wild pea (*Lathyrus aphaca*, Fig. 76, A) of S.F. Papilionaceae (Fam. Leguminosae) are modified leaves. (2) The tendrils of pea (*Pisum sativum*, Fig. 52, A) of S.F. Papilionaceae are modified terminal leaflets. (3) The tendrils of sarsaparilla (*Smilax macrophylla*, Fig. 76, G) of Fam. Liliaceae are regarded as modified stipules. (4) The tendrils of glory lily (*Gloriosa superba*, Fig. 76, B) of Fam. Liliaceae are modified leaf-apices. (5) The tendrils of passion flower (*Passiflora suberosa*, Fig. 76, C) of Fam. Passifloraceae may often be seen to correspond to the central flower of a dichasium or the first flower of a monochasium. (6) In Cucurbitaceae (Fig. 76, F), the tendrils have been considered by various authors* as roots, stems,

* A brief summary of the different views put forward regarding the morphological nature of tendrils in Cucurbitaceae is as follows :

Engler has shown that in *Kedrostis spinosa* the leaves possess thorn-like stipules, one of which grows out into a tendril. According to Payer, the tendril is formed due to a splitting of the petiole. Naudin suggests that the tendril is an extra-axillary branch at the side of the leaf and not in its axil. Braun and others hold that the tendril represents one of the bracteoles of the flower, the other on the opposite side being suppressed. Müller believes that the twining part of the tendril is the modified leaf, while the lower stiff portion is the stem-structure. Goebel is of opinion that the simple tendrils are the transformed prophylls of the axillary shoots; the branched tendrils are the compound tendrils, which are extra-axillary in position, and in which the lower portion of the tendril is the modified lateral branch, while the branches of the tendrils are the modified leaves.

leaves, stipules, shoots, flower-stalks or organs *sui generis*. (7) In *Vitis* sp. (Fam. Vitaceae, Fig. 76, H), the tendril represents the



FIG. 76. HOMOLOGY OF TENDRILS

A, of *Lathyrus* ; B, of *Gloriosa* ; C, of *Passiflora* ; D, of *Naravelia* ;
E, of *Cardiospermum* ; F, of *Cucurbita* ; G, of *Smilax* ; H, of *Vitis*.

main axis, which has been pushed aside by more vigorous growth of the branch borne in the axil of the opposed leaf. (8) The

tendrils of *Antigonon leptopus* (Fam. Polygonaceae), balloon vine (*Cardiospermum halicacabum*, Fig. 79, E) of Fam. Sapindaceae, etc., are modified inflorescence axes ; in the latter case, sometimes only the two lateral flowers of a dichasium are transformed into tendrils. (9) In *Clematis gouriana* (Fam. Ranunculaceae) the petiole is modified into a tendril, while in *Narvelia zeylanica* (Fig. 76, D) of Fam. Ranunculaceae, the tendril is the terminal leaflet modified. (10) In the majority of the members of Fam. Bignoniaceae the tendrils are modified rootlets.

Whatever be the origin of the tendrils*, they carry on the same function, i.e., climbing. Hence, all tendrils are analogous organs also.

HOMOLOGY OF DEFENSIVE ORGANS (THORNS, SPINES, ETC.)

(1) The thorns of glory of the garden (*Bougainvillea spectabilis*, Fig. 77, B) of Fam. Nyctaginaceae, *Duranta plumieri* (Fam. Verbenaceae), and wood apple† (*Aegle marmelos*, Fig. 77, A) of Fam. Rutaceae, etc., are modified branches. (2) The spines of sensitive plant (*Mimosa pudica*) and gum tree (*Acacia arabica*, Fig. 77, C) of S.F. Mimosae (Fam. Leguminosae), jujube (*Zizyphus jujba*, Fig. 77, D) of Fam. Rhamnaceae, etc., are modified stipules. (3) The spines of *Citrus* sp. (Fam. Rutaceae, Fig. 77, G) are modified first leaf or the first pair of leaves of axillary buds. (4) The spines of date palm (*Phoenix sylvestris*, Fig. 77, H) of Fam. Palmae, *Jacquinia ruscifolia* (Fig. 80, F) of Fam. Theophrastaceae, etc., are modified leaf-apices. (5) The spines on the fruit of water chestnut (*Trapa bispinosa*, Fig. 77, F) of Fam. Onagraceae, are the modified sepals. (6) The spines on the phylloclades of prickly pear (*Opuntia dillenii*, Fig. 77, E) of Fam. Cactaceae are modified leaves.

Whatever be the origin of these defensive organs, they carry on the same function of protection against animals. Hence, all spines and thorns (stem-spines) are analogous organs also.

* Besides the tendril, which is the chief climbing organ in plants, there are hooks, prickles, leaf-flagella, etc., which are different organs modified for the purpose of climbing.

† The morphological nature of the thorn of wood apple is, however, doubtful.

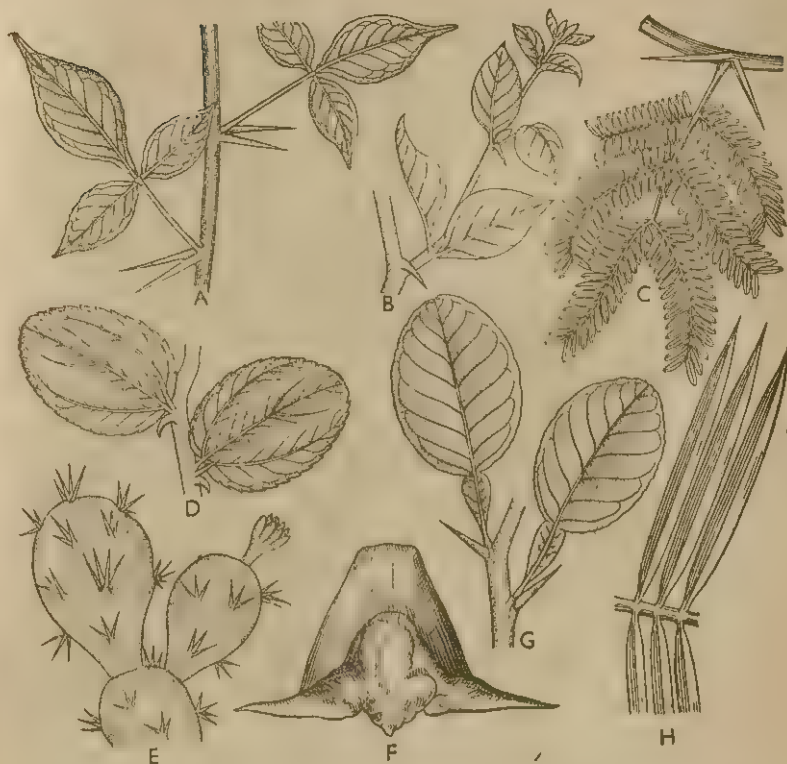


FIG. 77. HOMOLOGY OF DEFENSIVE ORGANS

A, thorns of *Aegle*; B, thorns of *Bougainvillea*; C, spines of *Acacia*; D, spines of *Zizyphus*; E, spines of *Opuntia*; F, spines of *Trapa*; G, spines of *Citrus*; H, spines of *Phoenix*.

HOMOLOGY OF STORAGE ORGANS (ROOTS, STEMS, ETC.)

(1) The tubers of sweet potato (*Ipomoea batatas*, Fig. 78, A) of Fam. Convolvulaceae, *Dahlia* sp. (Fam. Compositae), yam-bean (*Pachyrhizus angulatus*) of S.F. Papilionaceae (Fam. Leguminosae), etc., are modified roots. (2) The tubers of potato (*Solanum tuberosum*, Fig. 78, B) of Fam. Solanaceae, *Scirpus grossus* and *Cyperus rotundus* of Fam. Cyperaceae, artichoke (*Helianthus tuberosus*) of Fam. Compositae, etc., are modified branches. (3) The rhizomes of ginger (*Zingiber officinale*, Fig. 78, C) and turmeric (*Curcuma longa*) of Zingiberaceae, etc., and the corm of *Amorphophallus campanulatus* (Fig. 78, D) of Fam. Araceae, etc., are modified

stems. (4) The bulbils of *Dioscorea bulbifera* (Fig. 78, E) of Fam. Dioscoreaceae, *Lilium* sp. (Fam. Liliaceae), *Glozza bulbifera* (Fig. 78, F) of Fam. Zingiberaceae, etc., are modified buds.

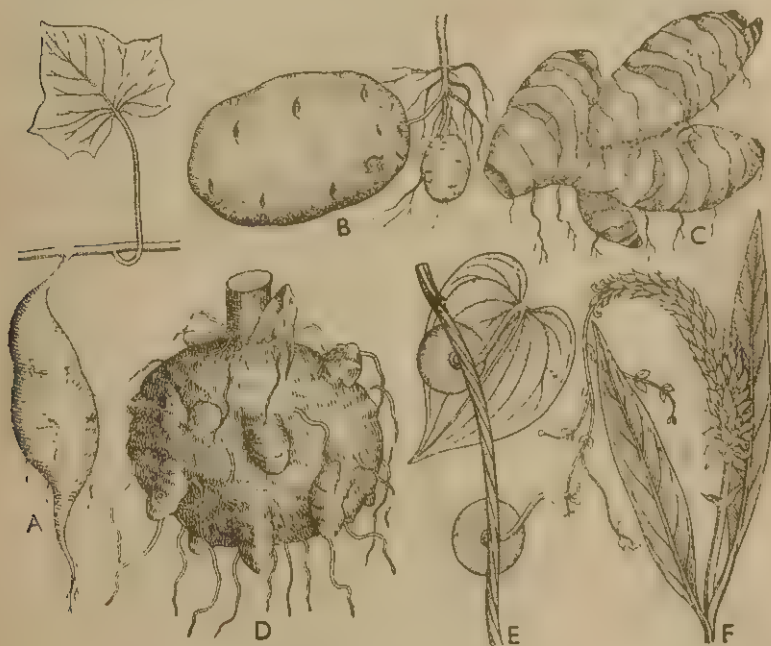


FIG. 78. HOMOLGY OF STORAGE ORGANS

A, tuberous root of *Ipomoea*; B, stem-tuber of *Solanum*; C, rhizome of *Zingiber*; D, corm of *Amorphophallus*; E, bulbils of *Dioscorea*; F, bulbils of *Glozza*.

Whatever be the origin of the storage organs, they all carry on the same function of storage. Hence, all storage organs are also analogous organs.

HOMOLGY OF PHOTOSYNTHETIC ORGANS (STEMS, PETIOLES, ETC.)

(1) The phylloclades of whip tree (*Casuarina equisetifolia*, Fig. 79, A), of Fam. Casuarinaceae, *Muehlenbeckia platyclados* (Fig. 79, C) of Fam. Polygonaceae, prickly pear (*Opuntia dillenii*, Fig. 79, B), of Fam. Cactaceae, *Vitis quadrangularis* (Fig. 79, E) of Fam. Vitaceae, *Euphorbia antiquorum* and

E. tirucauli of Fam. Euphorbiaceae, etc., are metamorphosed stems. (2) The cladodes of *Asparagus racemosus* (Fig. 79, D) of Fam. Liliaceae are also metamorphosed stems. (3) The phyllodes of *Acacia moniliformis* (Fig. 79, G) of S.F. Mimosae (Fam. Leguminosae) are modified petioles. (4) The leafy bodies found in wild pea (*Lathyrus aphaca*, Fig. 79, F) of S.F. Papilionaceae (Fam. Leguminosae) are modified stipules.



FIG. 79. HOMOLOGY OF PHOTOSYNTHETIC ORGANS
Phylloclades of *Casuarina* (A), *Opuntia* (B), *Muehlenbeckia* (C), and *Litis* (E); D, cladodes of *Asparagus*; F, foliaceous stipules of *Lathyrus*; G, phyllode of *Acacia*.

Whatever be the origin of the photosynthetic organs, they carry on the same function of photosynthesis. Hence, all photosynthetic organs are also analogous organs.

DEFENSIVE ORGANS OF PLANTS

Plants are generally attacked by the herbivorous animals for the sake of food. Hence, to protect themselves, they are provided with armatures, *i.e.*, weapons of defence, or they have some other special devices.

A. ARMATURES OF PLANTS

The armatures of plants may be thorns, spines, prickles, stinging hairs and glandular hairs.

Thorns or stem-spines are metamorphosed stems or branches, which are sub-epidermal in origin. These are hard, pointed structures and may be simple or branched. Thorns are commonly found in wood apple (*Aegle marmelos*, Fig. 77, A) of Fam. Rutaceae, *Randia dumetorum* (Fam. Rubiaceae), *Duranta plumieri* (Fam. Verbenaceae), glory of the garden (*Bougainvillea spectabilis*, Fig. 77, B) of Fam. Nyctaginaceae, *Flacourita cataphracta* (Fam. Bixaceae), *Alangium lamackii* of Fam. Alangiaceae, *Hygrophila spinosa* (Fam. Acanthaceae, Fig. 80, A), *etc.* Many trees are provided with thorns only at the lower parts, which are liable to be attacked by the animals.

Spines are modified leaves or parts of leaves. These are sharp needle-like structures and are commonly found in pineapple (*Ananasa sativa*) of Fam. Bromeliaceae, gum tree (*Acacia arabica*, Fig. 77, C) of S.F. Mimosae (Fam. Leguminosae), Mexican poppy (*Argemone mexicana*, Fig. 80, E) of Fam. Papaveraceae, lemon (*Citrus limon*, Fig. 77, G) of Fam. Rutaceae, date palm (*Phoenix sylvestris*, Fig. 77, H) of Fam. Palmae, *Jacquinia ruscifolia* (Fam. Theophrastaceae, Fig. 80, F), *etc.* It has been found that the phylloclade of prickly pear (*Opuntia dillenii*, Fig. 79, B) of Fam. Cactaceae, which is beset with numerous spines all over its surface, when given to cows or other animals, is left untouched, but when the spines are removed, the animals readily feed on it. The spines of *Acacia* and some other plants are directed upwards in their early stage, but afterwards when the plants attain certain heights, the spines are directed outwards; finally, when they are fully formed the spines are directed downwards. This clearly shows that plants are able to defend themselves against animals by means of spines.

Prickles are curved or straight, sharp-pointed structures, which arise superficially at any point from the stem, branch, leaf, fruit, etc. These are commonly found in rose (*Rosa centifolia*, Fig. 80, B) of Fam. Rosaceae, *Solanum xanthocarpum* (Fam. Solanaceae), *Lantana camara* (Fam. Verbenaceae), *Zizyphus oenopia* (Fam. Rhamnaceae), fever nut (*Caesalpinia bonducella*) of S.F. Caesalpinieae (Fam. Leguminosae), etc.

Stinging hairs are developed on the leaves and stems of stinging nettles (*Urtica dioica* and *Fleurya interrupta* of Fam.



FIG. 80 DEFENSIVE ORGANS

A, thorns of *Hygrophila* ; B, prickles of *Rosa* ; C, myrmecophily in *Acacia* ; D, glandular hairs on fruits of *Plumbago* ; E, spiny leaf-margin in *Argemone* ; F, spiny leaf-apex in *Jacquinia* ; G, mimicry in *Arisaema*.

Urticaceae and *Tragia involucrata* of Fam. Euphorbiaceae), or on the fruits of *Mucuna pruriens* of S.F. Papilionaceae (Fam. Leguminosae). These hairs contain formic acid. Whenever the hairs come in contact with the skin of a passerby, their tips are broken and the acid is injected into the puncture producing a burning sensation.

Glandular hairs are produced on the leaves, stems and fruits of plants, such as *Jatropha curcas* and *J. gossypifolia* of Fam. Euphorbiaceae, *Plumbago zeylanica* (Fig. 80, D) of Fam. Plumbaginaceae, etc. These hairs secrete sticky substances. Whenever an animal attempts to feed upon the plants, the hairs adhere to its mouth and make it difficult to brush them off. Thus, these plants are saved from the ravages of the animals.

A dense covering of hairs on the body of plants, as in *Calotropis procera* (Fam. Asclepiadaceae), is always repulsive to animals.

B. OTHER DEVICES FOR DEFENCE

Plants may defend themselves against animals by the following devices also.

Taste. Many plants such as bitter gourd (*Momordica charantia*) of Fam. Cucurbitaceae, margosa (*Melia azadirachta*) of Fam. Meliaceae, ginger (*Zingiber officinale*) of Fam. Zingiberaceae, *Vitex negundo* (Fam. Verbenaceae), etc., can protect themselves against animal attacks by possessing bitter taste.

Odour. Some plants, such as basil (*Ocimum* sp.) of Fam. Labiatae, *Clerodendron infortunatum* and *Lantana camara* of Fam. Verbenaceae, *Poederia foetida* (Fam. Rubiaceae), etc., are able to ward off the attacks of animals by means of repulsive odour.

Poisonous substances. Many plants store up poisonous substances in their bodies or in the bark, and thus these are discarded by animals. Familiar examples are tobacco (*Nicotiana tabacum*) and thorn apple (*Datura fastuosa*) of Fam. Solanaceae, *Cinchona succirubra* (Fam. Rubiaceae), oleander (*Nerium odorum*) and *Thevetia peruviana* (= *T. nerifolia*) of Fam. Apocynaceae, etc.

Waste products. Some plants, such as arum (*Colocasia antiquorum*), and *Alocasia indica* of Fam. Araceae contain waste products, such as raphides, and thus these are avoided by animals.

Mimicry. Certain plants assume the general appearance of serpents or other threatening animals, or even of inanimate objects, and thus these are avoided by the grazing animals. Such an adaptation is known as **mimicry**. There is a species of arum (*Arisaema speciosa*, Fig. 80, G), growing in Darjeeling, whose body is spotted like a snake, and it has a long tail-like structure and a hood-like spathe, so that the whole plant looks like a cobra from a distance. The grazing animals usually think it to be a real serpent and turn away from it. Similarly, the Rangoon potatoes may be mistaken for clods of earth from a distance, and thus they are passed unnoticed.

Myrmecophily. Many plants, such as mango (*Mangifera indica*) of Fam. Anacardiaceae, litchi (*Litchi chinensis*) of Fam. Sapindaceae, rose-apple (*Eugenia jambos*) of Fam. Myrtaceae, *Acacia sphaerocephala** (Fig. 80, C) of S.F. Mimosae (Fam. Leguminosae), *Korthalsia horrida* (Fam. Palmae), etc., give shelter or food to various kinds of stinging insects, such as red ants, wood-ants, etc. Whenever any animal attacks them, the insects rush towards the enemy, sting it mercilessly and drive it away. Thus, the insects act as bodyguards to ward off the attacks of animals, and the plants are able to defend themselves with their help. Such an adaptation is known as **myrmecophily**, and the plants are said to be **myrmecophilous**.

* Myrmecophily was discovered for the first time in this plant in 1893.

CHAPTER V

THE FLOWER

Though it is conventional to consider the 'flowers' as characteristic of angiosperms alone, yet it is extremely difficult to define the structure properly. Basically, a flower consists of a **receptacle**, the stem tip, on which are borne both the sterile as well as fertile appendages. The receptacle possesses nodes and internodes, just like an ordinary vegetative shoot. In case of the flower, however, the internodes are generally suppressed, and consequently, the nodes are very closely crowded together. The appendages may be borne either completely spirally or in whorls or partly in spirals and partly in whorls. When in spirals, the floral appendages generally follow the rules of phyllotaxy of foliage leaves, and this is usually referred to as '**floral phyllotaxy**'.

A flower having appendages in whorls is said to be a **cyclic** one, while that with spirally arranged appendages is **acyclic**. Mustard (*Brassica nigra*) of Fam. Cruciferae, brinjal (*Solanum melongena*) of Fam. Solanaceae, etc., are examples of cyclic flowers, and *Ranunculus* sp. (Fam. Ranunculaceae), lotus (*Nelumbo nucifera*=*Nelumbium speciosum*) of Fam. Nymphaeaceae, etc., are acyclic ones. In other cases, where some of the appendages are arranged in whorls, while others are in spirals, the flowers are said to be **hemicyclic**, as in water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae.

It has already been pointed out that, when the plant attains maturity, it reproduces sexually and the organs of sexual reproduction are formed. The flower is the most conspicuous structure which is intimately connected with the process of sexual reproduction in the higher plants, resulting in the formation of fruits and seeds.

The flower can thus be conveniently regarded as a condensed, modified shoot bearing a collection of fertile appendages of sporophylls, either *microsporophylls* (*stamens*), or *megasporophylls* (*carpels*), or both, with or without one or two sets of sterile

appendages or accessory whorls,* and is meant for the purpose of sexual reproduction

Flowers develop on a stem or a branch either in a terminal or in an axillary position.

A complete flower (Fig. 81) consists of the following four parts.

Calyx is the outermost and lowermost set and is composed of green leaf-like structures, called **sepals**; **corolla** is the next inner and upper set and is composed of usually brightly coloured leafy structures, called **petals**; **androecium**† is the third inner and upper set and is composed of **stamens** or **microsporophylls**, which produce **pollen grains** or **microspores**; **gynaecium**‡ or **pistil** is the innermost and uppermost set and is composed of **carpels** or **megasporophylls**, which bear another type of spores, called **megaspores**.

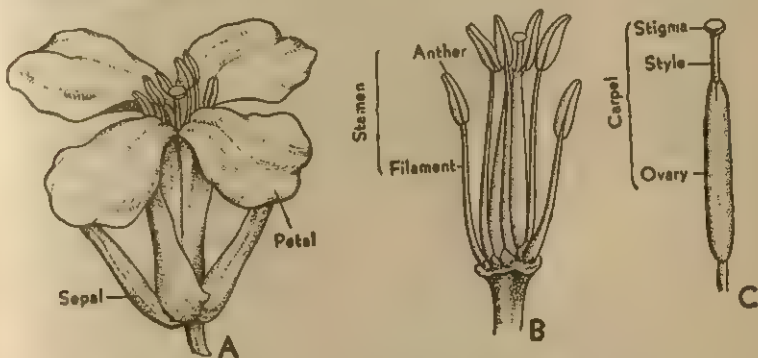


FIG. 81. PARTS OF A COMPLETE FLOWER

A, an entire flower; B, androecium; C, gynaecium.

All the four floral sets are inserted on a very short axis, called the **thalamus** or **receptacle**. Of these four sets the androecium and the gynaecium are the **essential sets**, because these are absolutely necessary for reproduction. The calyx and the corolla are the **accessory sets**, as these form the floral envelopes and are not directly concerned with the reproduction of the plant.

* The accessory whorls of floral members are usually differentiated into **calyx** (consisting of *sepals*) and **corolla** (made up of *petals*). When these are not differentiable, they are called *perianths*.

† Also spelt as *androecium*.

‡ Also spelt as *gynoecium* or *gynoeceum*.

Flowers are extremely variable as to the number and shape of the individual members that enter into their structure. A **complete flower** is one, in which all the four sets of floral members are present ; if any of these sets are lacking, it is **incomplete**. Rose (*Rosa centifolia*) of Fam. Rosaceae, China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, etc., are examples of complete flowers, while tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae, gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, etc., are examples of incomplete flowers.

When both stamens and carpels are present in a flower, it is said to be **perfect** or **bisexual** or **hermaphrodite** or **monoclinous**,



FIG. 82. UNISEXUAL FLOWERS OF *Cucurbita*
A, male flower ; B, female flower.

as in thorn apple (*Datura fastuosa*) of Fam. Solanaceae, lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae, etc. If the flower lacks either stamens or carpels, it is said to be **imperfect** or **unisexual** or **diclinous**, as in gourd (*Cucurbita maxima*, Fig. 82), cucumber. (*Cucumis*

sativus) and other plants of Fam. Cucurbitaceae, as well as plants belonging to the Fams. Sapindaceae, Euphorbiaceae, Urticaceae, Araceae, Palmae, etc.

In case of unisexual flowers, either stamens or carpels only may be present; in the former type, the flowers are known as **staminate** or **male** flowers, and in the latter, as **pistillate** or **female** ones. If a flower contains neither stamens nor any carpel, it is said to be **neuter**. If staminate and pistillate flowers are borne on the same plant, it is called **monoecious**, as in most plants of Fam. Cucurbitaceae and Euphorbiaceae, maize (*Zea mays*) of Fam. Gramineae, palmyra palm (*Borassus flabellifer*) of Fam. Palmae etc. But, if the staminate flowers are produced on one

plant and the pistillate ones on another, the plants are said to be **dioecious**, as in palwal (*Trichosanthes dioica*) and *Bryonia dioica* of Fam. Cucurbitaceae, papaw (*Carica papaya*) of Fam. Caricaceae, date palm (*Phoenix sylvestris*) of Fam. Palmae, etc. When the staminate, pistillate and hermaphrodite flowers are developed on the same plant, it is said to be **polygamous**, as in mango (*Mangifera indica*) of Fam. Anacardiaceae.

When both calyx and corolla are present in a flower, it is known as **dichlamydeous**; when, with a simple perianth, it is **monochlamydeous**; and when without a perianth, **achlamydeous**. Rose (*Rosa centifolia*) of Fam. Rosaceae, mustard (*Brassica nigra*) of Fam. Cruciferae, brinjal (*Solanum melongena*) of Fam. Solanaceae, etc., are examples of dichlamydeous flowers. Four o'clock plant (*Mirabilis jalapa*) and other plants of Fam. Nyctaginaceae, tuberose (*Polianthes tuberosa*) and other plants of Fam. Amaryllidaceae, glory lily (*Gloriosa superba*) and other plants of Fam. Liliaceae, etc., afford examples of monochlamydeous flowers, while flowers of betel vine (*Piper betle*), long pepper (*Piper longum*) and other plants of Fam. Piperaceae, etc., are achlamydeous ones.

A flower is said to be **regular**, when individual members of each set are of the same shape, size and colour; if otherwise, it is **irregular**.

A flower is said to be **trimerous**, when the number of floral members in each whorl is three or any multiple of it, as is found in the monocotyledonous plants and a few dicotyledonous ones, such as *Magnolia grandiflora*, *Michelia champaca* and other plants of Fam. Magnoliaceae, custard apple (*Anona squamosa*) and other plants of Fam. Anonaceae, as well as plants belonging to Fams. Menispermaceae, Berberidaceae, etc., it is **tetramerous**, when the number of floral members in each whorl is four or any multiple of it, as in the mustard (*Brassica nigra*), radish (*Raphanus sativus*) and other plants of Fam. Cruciferae, *Polanisia icosandra* (= *Cleome viscosa*), *Gynandropsis gynandra* (= *G. pentaphylla*) and other plants of Fam. Capparidaceae, *Scoparia dulcis* (Fam. Scrophulariaceae), sensitive plant (*Mimosa pudica*) and other plants of S.F. Mimosae (Fam. Leguminosae), etc.; and it is **pentamerous**, when the number

of floral members in each whorl is five or any multiple of it, as in most of the dicotyledonous plants.

The growth of the floral axis terminates with the production of the gynaecium, but where it (axis) continues to grow on, even after the formation of the gynaecium, the flower is said to be a **proliferous** one, as in monstrous flowers. This phenomenon is known as **proliferation**.

In case of an axillary flower, the bract is situated in 'front of' and the axis 'behind' it, so that half of the flower which faces the bract is called the **anterior** part, and the remaining half facing the axis is the **posterior** one. Thus, in this case, a vertical plane will divide the axis, the flower and the bract into two halves in the **median** or **antero-posterior** plane.

As regards the symmetry of the flowers, a flower may be **actinomorphic** or radially symmetrical, when it may be cut into two equal halves along any plane passing through the centre, as in China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, radish (*Raphanus sativus*) of Fam. Cruciferae, etc., **zygomorphic** or bilaterally symmetrical, when symmetrical in one plane only, as in pea (*Pisum sativum*), *Sesbania grandiflora* and other plants of S.F. Papilionaceae (Fam. Leguminosae) snapdragon (*Antirrhinum majus*) of Fam. Scrophulariaceae, *Brunfelsia americana* (Fam. Solanaceae), etc., and **asymmetrical** or irregularly symmetrical, when not symmetrical in any plane, as in Indian shot (*Canna indica*) of Fam. Cannaceae, orchids (Fam. Orchidaceae), etc.

The majority of modern morphologists regard a complete flower as the primitive type. Any deviation from this involving a reduction or suppression of one of the floral components leads to the development of an advanced type. A flower, in which either the stamens are represented by staminodes or the pistils by pistillodes, is considered to indicate a definite phyletic line of advancement. Such a type of reduction in the androecial or gynaecial elements may be either partial or complete. When the reduction is complete, the flower is unisexual, and is either staminate or pistillate as the case may be. In extreme cases, both the stamens and pistils are completely suppressed, or, even if present, are so highly reduced that they are practically non-existent and non-functional, as in *Hydrangea* (Fam. Saxifragaceae),

Viburnum (Fam. Caprifoliaceae), and some members of Fam. Compositae. Though such flowers are usually described as sterile or neutral flowers, morphologically they cannot be regarded as flowers at all, as they do not possess any reproductive element. The following table will give some idea about the present-day concept of the *primitive* and *advanced* types of flowers :

| Primitive flower | Advanced flower |
|---|--|
| 1. Actinomorphic (<i>i.e.</i> , radially symmetrical). | Zygomorphic (<i>i.e.</i> , bilaterally symmetrical) or asymmetrical. |
| 2. With four sets of floral appendages. | With only one set of floral appendage. |
| 3. Appendages spirally arranged on the receptacle. | Appendages arranged in whorls on the receptacle. |
| 4. Floral parts indefinite in number and all free. | Floral parts few and definite in number, as well as connate or adnate. |

It is interesting to note, however, that the viewpoint, embodied in the above table, is in complete opposition to that propounded by Engler, whose system of classification of plants is still followed in a large number of herbaria throughout the world. Consequently, basing on this modern concept, plant groups, so long believed to be primitive ones, are at present considered as decidedly advanced.

The mode of appearance of the floral parts is almost similar to that of the leaves on a stem- or branch-apex. On making a longitudinal section through a very young and developing flower bud, it is found that the different floral parts appear at first as minute knob-like masses of meristems at the apex of the receptacle. Generally, the sequence of development is acropetal, and the sepals, petals, stamens, and carpels appear in succession. The apical meristem, however, does not remain as such for an indefinite length of period, but it is ultimately converted into carpels. This type of development of floral parts can be found in Indian buttercup (*Ranunculus sceleratus*, Fig. 83) of Fam. Ranunculaceae. Deviations from this are also frequently met with, for example, in shepherd's purse (*Capsella*

bursa-pastoris, Fig. 84), of Fam. Cruciferae the petals appear last, in fleabane (*Erigeron* sp.) and some other members of the

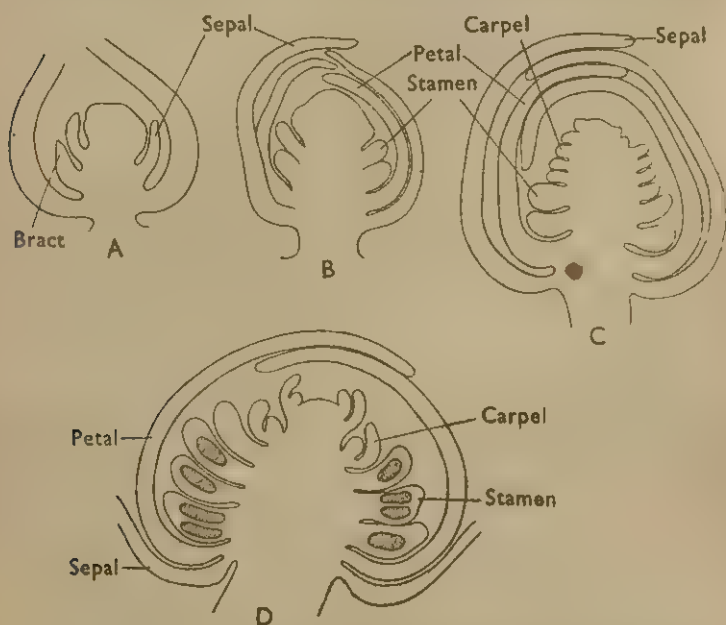


FIG. 83. A—D, GRADUAL STAGES IN DEVELOPMENT OF FLORAL PARTS IN *Ranunculus*.

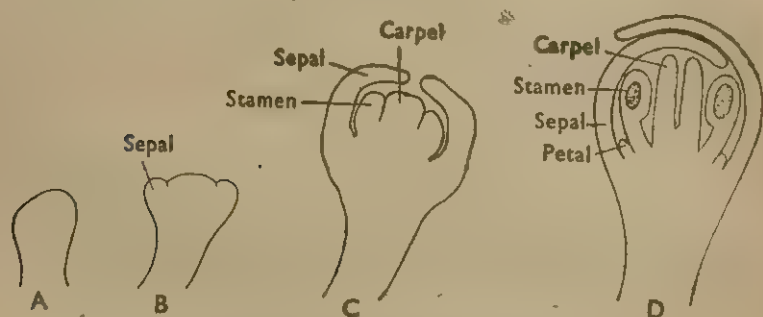


FIG. 84. A—D, GRADUAL STAGES IN DEVELOPMENT OF FLORAL PARTS IN *Capsella*.

Fam. Compositae the sepals develop last of all and remain vestigial.

The flower is equivalent to a modified shoot (Fig. 85).

The flower may be regarded as equivalent to a modified shoot. This can be proved by the following facts.

Axis-nature of the thalamus. The axis-nature of the thalamus is evident from the fact, that it consists of nodes and internodes. The internodes are usually suppressed, hence all floral leaves appear to arise from the same place. In spider flower (*Gynan-*

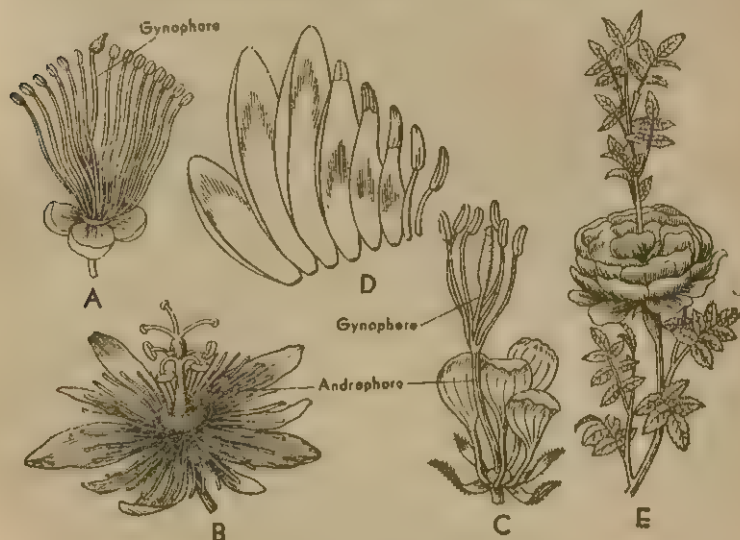


FIG. 85

A, a flower of *Capparis*; B, a flower of *Passiflora*; C, a flower of *Gynandropsis*; D, gradual transition of floral leaves in *Nymphaea*; E, a monstrous flower of rose.

dropsis gynandra = *Gynandropsis pentaphylla*, Fig. 85, C) and *Capparis sepiaria* (Fig. 85, A) of Fam. Capparidaceae, passion flower (*Passiflora suberosa*, Fig. 85, B) of Fam. Passifloraceae, *Pterospermum acerifolium* (Fam. Sterculiaceae), etc., one or more internodes of the thalamus are elongated resembling a branch, thus separating the different sets of floral members, from one another. In *Michelia champaca* (Fam. Magnoliaceae), the carpellary region of the conical thalamus elongates during the fruiting stage. In monstrous roses (Fig. 85, E) and sometimes in pears, the thalamus shows monstrous develop-

ment. In each of these cases, the organic apex of the thalamus, which usually remains suppressed and surrounded by carpellary leaves, grows to prove its axis-nature like the shoot-apex.

Leaf-nature of the floral members. The leaf-nature of the floral members is evident from the fact, that they show peculiar modifications and transitional stages in many cases. Sepals are usually flat and green, but are sometimes coloured, as in *Michelia champaca* (Fam. Magnoliaceae). Like leaves, they possess stomata, and venations, and their margins are sometimes toothed, as in rose (*Rosa centifolia*) of Fam. Rosaceae, *Gardenia florida* (Fam. Rubiaceae), etc., but they differ from leaves in being absolutely sessile. In *Mussaenda frondosa* (Fig. 87 of Fam. Rubiaceae)*, one of the sepals is transformed into a distinctly yellowish coloured petaloid structure. In roses, it is sometimes found that one or more segments of the calyx are transformed into ordinary compound leaves, thus proving its leaf-nature. Petals, though coloured, have some resemblance to leaves ; they show characteristic venation and in some roses (green roses) and some varieties of larkspur (*Delphinium ajacis* of Fam. Ranunculaceae), the petals are green. Whether green or coloured otherwise, they have structures and forms similar to those of leaves. The difficulty arises in case of the stamens and carpels, as these are unlike leaves in all respects. But the leaf-nature can even be made out by examining certain flowers. That stamens are also equivalent to leaves can be inferred from the following facts : a gradual transition is observed from petals to stamens, as in the white water lily (*Nymphaea stellata*, Fig. 85, D) of Fam. Nymphaeaceae ; the stamens of Indian shot (*Canna indica*) of Fam. Cannaceae are petaloid ; frequent transformation of stamens into petals, as in garden rose (Fam. Rosaceae), China rose (*Hibiscus rosa-sinensis*) and changeable rose (*H. mutabilis*) of Fam. Malvaceae, etc., may be seen.† The so-called 'double flowers' of jasmines (*Jasminum sambac*, *J. auriculatum*) of Fam. Oleaceae, *Clitoria ternatea* of S.F. Papilionaceae (Fam. Leguminosae), *Gradenia florida* (Fam. Rubiaceae), etc., are also due to the metamorphosis of stamens into petals. The carpels are also equivalent to leaves, because sometimes

* In *M. philippica*, all the sepals are coloured. In *Pogonopus* (Fam. Rubiaceae) one of the sepals is coloured scarlet red.

† This phenomenon is known as the 'doubling' of flowers.

in the roses, particularly in green roses, the carpels are transformed into green leaves ; the carpels become petaloid, as in Indian shot (*Canna indica*) of Fam. Cannaceae, or may be metamorphosed into petals, as in *Zinnia* sp. (Fam. Compositae) under cultivation. In S.F. Papilionaceae (Fam. Leguminosae), the ovary is made up of a single folded greenish carpel, often showing a distinct midrib and prominent veins. All these transitional forms tend to show the foliar nature of the floral members.

The floral members differ from the foliage leaves by the fact that they do not normally bear any bud in their axils, but sometimes such buds do occur. This is the reason why a flower is found within a flower, as in *Jasminum auriculatum* (Fam. Oleaceae), or a fruit within a fruit, as in palwal (*Trichosanthes dioica*) of Fam. Cucurbitaceae, papaw (*Carica papaya*) of Fam. Caricaceae, etc., or a shoot growing on the top of a fruit, as in pear (*Pyrus communis*) of Fam. Rosaceae.

THE FLORAL PARTS

THE RECEPTACLE (THALAMUS)

It has already been pointed out that the receptacle or thalamus is the short floral axis, with compressed nodes and internodes, on which the various floral leaves are inserted. In a few cases, however, the internodes become elongated and distinct. The elongated internode between the calyx and the corolla is the **anthophore**, which represents the first internode, as in *Silene* sp. and a few other plants of Fam. Caryophyllaceae ; the second internode, i.e., the internode between the corolla and the androecium, is called the **androphore**, as in spider flower (*Gynandropsis gynandra* = *G. pentaphylla*) of Fam. Capparidaceae, passion flower (*Passiflora suberosa*) of Fam. Passifloraceae, etc., the third internode, i.e., the internode between the androecium and the gynaecium, is called the **gynophore**, as in *Pterospermum acerifolium* (Fam. Sterculiaceae), *Polanisia icosandra* (= *Cleome viscosa*), *Gynandropsis gynandra* (= *G. pentaphylla*) and *Capparis sepiaria* of Fam. Capparidaceae, some members of Fam. Anacardiaceae, etc. When both androphore and gynophore are present, as in *Gynandropsis*, they constitute the **gynandrophore** or **androgynophore**.

In some cases, the thalamus forms a ring or cushion-like structure, known as the **disc**, at the base of the ovary. as in members of Fams. Oxalidaceae, Rutaceae, Meliaceae, Vitaceae, Sapindaceae, Anacardiaceae, etc.

When the thalamus is prolonged beyond the ovary, it is called the **carpopophore**, as in coriander (*Coriandrum sativum*), anise (*Foeniculum vulgare*), and the other plants of Fam. Umbelliferae, wood sorrel (*Oxalis corniculata*) of Fam. Oxalidaceae, balsam (*Impatiens balsamina*) of Fam. Balsaminaceae, etc.

The form of thalamus is variable. Thus, it is slightly *convex* in cotton (*Gossypium herbaceum*) of Fam. Malvaceae, brinjal (*Solanum melongena*) of Fam. Solanaceae, etc., more or less *flat* in pea (*Pisum sativum*), and other plants of S.F. Papilionaceae (Fam. Leguminosae); *filiform* in *Gynandropsis gynandra* (= *G. pentaphylla*) of Fam. Capparidaceae; *elongated* or *conical* in *Michelia champaca* (Fam. Magnoliaceae), custard apple (*Anona squamosa*) of Fam. Anonaceae, etc., *concave* or *cup-like* in rose (*Rosa centifolia*) of Fam. Rosaceae; *spongy* and *top-shaped* in lotus (*Nelumbo nucifera*=*Nelumbium speciosum*) of Fam. Nymphaeaceae.

INSERTION OF FLORAL LEAVES ON THE THALAMUS

The different sets of floral leaves are inserted on the thalamus as follows :

Hypogyny (Fig. 86, A & B). When the thalamus is con-

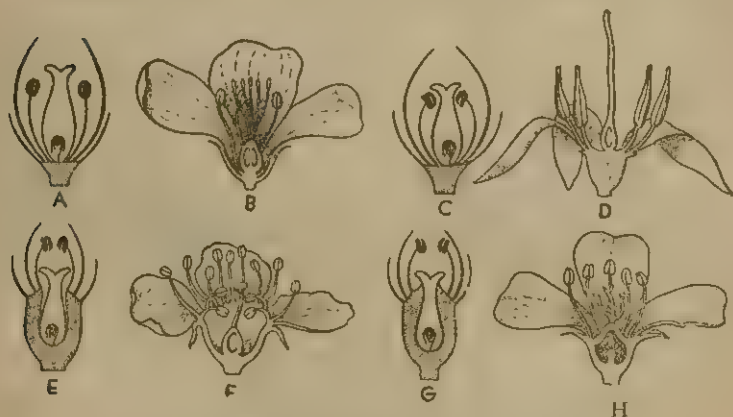


FIG. 86. INSERTION OF FLORAL LEAVES ON THALAMUS

A-B, Hypogyny ; C-F, Perigyny ; G-H, Epigyny.

vex or elongated, the carpel or carpels occupy the topmost position on it, and other floral members (stamens, petals, and sepals) are successively inserted below the same, the mode of arrangement is called **hypogyny**, and the flower is said to be **hypogynous**. The ovary is said to be **superior** in this case. Common examples are mustard (*Brassica nigra*) of Fam. Cruciferae, China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, brinjal (*Solanum melongena*) of Fam. Solanaceae, custard apple (*Anona squamosa*) of Fam. Anonaceae, etc.

Perigyny (Fig. 86, C-F). When the thalamus is flat or slightly cup-shaped, the carpel or carpels are situated at its centre, and other floral members (stamens, petals, and sepals) are inserted on its margin, the mode of arrangement is called **perigyny**, and the flower is said to be **perigynous**. In this case, the ovary is still described as **superior***, as in pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae), rose (*Rosa centifolia*) of Fam. Rosaceae, *Portulaca oleracea* (Fam. Portulacaceae), etc.

Epigyny (Fig. 86, G & H). When the thalamus is cup-shaped as in some perigynous flowers, and the lower part of the ovary is not only concealed in the concavity but also fused with the inner wall of the thalamus, and other floral members (stamens, petals, and sepals) appear to be inserted upon the ovary, the mode of arrangement is called **epigyny**, and the flower is then described as **epigynous**. The ovary is said to be **inferior** in this case. Common examples are gourd (*Cucurbita maxima*) and other plants of Fam. Cucurbitaceae, sunflower (*Helianthus annuus*) and other plants of Fam. Compositae, *Ixora parviflora* and other plants of Fam. Rubiaceae, tuberose (*Polianthes tuberosa*) and other plants of Fam. Amaryllidaceae, guava (*Psidium guayava*) and other plants of Fam. Myrtaceae, *Hydrocotyle asiatica* and other plants of Fam. Umbelliferae, orchids (Fam. Orchidaceae), *Musa* sp., *Canna* sp., *Zingiber* sp., and other plants of the Order Scitamineae, *Belamcanda chinensis* and other plants of Fam. Iridaceae, etc.

* An ovary, which is somewhat intermediate in position in between the superior and the inferior ovaries, is referred to as **half inferior** or **sub-inferior**, as is found in Fam. Melastomaceae. On the other hand, the ovary apparently seems to be inferior in position in flowers of marvel of Peru (*Mirabilis jalapa*) and *Boerhaavia repens* of Fam. Nyctaginaceae; such an ovary may be termed as **pseudo-inferior**.

It is generally accepted that the inferior ovary has been evolved from the superior one, and there are two theories trying to explain such an evolution. The older of these two theories is known as the **receptacular theory**. According to this theory, the inferior ovary lies embedded within or surrounded by a receptacular tissue, which is usually tube-like, or cup-like in appearance. On the other hand, in flowers having inferior ovary, the ovary remains surrounded by another type of cylindrical tube-like or cup-shaped receptacular tissue, called the **hypanthium**. But recent anatomical studies by Eames (1931), Jackson (1934), and MacDaniels (1937) have proved that the so-called receptacular tissues (in most of the flowers having inferior ovaries or superior ovaries within the hypanthia) are not receptacular in origin, but are formed by the fusion of some appendicular or foliar structures. The second theory is called the **appendicular theory**. This theory holds that the tissues lying adnate to the inferior ovary and the hypanthium surrounding the superior ovary are, in the majority of instances, homologous structures, and are appendicular in origin (*i.e.*, they are components of the flower and not of the receptacle). The present-day inferior ovary might have originated in two ways : (i) by the union of the other floral elements, like calyx, corolla, or androecium to the wall of the ovary, and (ii) by a depression and marginal expansion of the receptacle as well as its enveloping and adnation to the ovary. Wilson and Just (1939) are of opinion that though the inferior ovary is advanced and derived from the superior one, "epigynous and perigynous flowers differ in no essential respect from the hypogynous condition; the inferior ovary is, in most cases at least, appendicular in origin, not receptacular".

THE PERIANTH

The flowers of monocotyledonous plants in general possess a **perianth**, where there is no distinction between calyx and corolla. In grasses (Fam. Gramineae), the perianth is very simple in construction, where it is more or less scale-like, and is known as the **lodicule**. Sometimes, the perianth is membranous and persistent, as in the members of Fam. Amaranthaceae. But in some families of monocotyledons, the perianth is highly developed and sometimes brightly coloured, and is called the

petaloid perianth, as in glory lily (*Gloriosa superba*) of Fam. Liliaceae, tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae, water hyacinth (*Eichhornia crassipes*) of Fam. Pontederiaceae, *Commelina benghalensis* (Fam. Commelinaceae), *Iris nepalensis* (Fam. Iridaceae), etc. Some families of dicotyledons also have petaloid perianth, as in *Polygonum plebeium*, *Antigonon leptopus* and some other plants of Fam. Polygonaceae, marvel of Peru (*Mirabilis jalapa*) and *Boerhaavia repens* of Fam. Nyctaginaceae, *Acalypha hispida* (Fam. Euphorbiaceae), etc. In some species of *Polygonum* (Fam. Polygonaceae), *Acalypha indica*, *Phyllanthus niruri* and many other plants of Fam. Euphorbiaceae, *Bougainvillea spectabilis* (Fam. Nyctaginaceae), *Chenopodium* sp. and other members of Fam. Chenopodiaceae, and some lilies, like *Paris polyphylla* of Fam. Liliaceae, the perianth is **sepaloid**. When the perianth members are separated from one another, they are said to be **polyphyllous**, as in *Polygonum* sp. (Fam. Polygonaceae), *Asparagus racemosus*, glory lily (*Gloriosa superba*) and some other plants of Fam. Liliaceae, but when united, **gamophyllous**, as in *Boerhaavia repens* and other plants of Fam. Nyctaginaceae, *Crinum asiaticum*, tuberose (*Polianthes tuberosa*) and some other plants of Fam. Amaryllidaceae, etc. The function of the perianth leaves is to protect the young essential sets, but when brightly coloured, to attract insects for pollination.

THE CALYX

The calyx is the lowest and outermost accessory set of floral members, and consists of **sepals**. The sepals are usually flat and green, but sometimes become brightly coloured, and are then said to be **petaloid** or **petaline**, as in peacock flower (*Caesalpinia pulcherrima*) and *Saraca indica* of S.F. Caesalpinieae (Fam. Leguminosae), cumin (*Nigella sativa*) of Fam. Ranunculaceae, etc. In *Mussaenda frondosa* (Fam. Rubiaceae, Fig. 87) one of the sepals is transformed into a large, white or yellow, leafy structure, while in *Pogonopus* sp. (Fam. Rubiaceae), it is scarlet red. In *Mussaenda philippica*, however, all the five sepals are large and petaloid. Like leaves, they possess stomata and venation, and often have serrated margins.

The primary function of the calyx is protective, *i.e.* it protects the inner parts of the flower from mechanical injury, excessive sunshine and rain, and from drying out in the bud condition.



FIG. 87. PETALOID SEPAL
OF *Mussaenda*.

For this reason, the sepals possess a more firmer structure than other floral members. Being green in colour, it can also perform the photosynthetic function. Besides these, it sometimes performs special functions. When petaloid or coloured otherwise, it performs the function of attracting insects for pollination; as pappus, it helps in the dispersal of fruits, and when spiny, its function is defensive.

The calyx may be **regular** or **irregular**. When the sepals are free from one another, the calyx is said to be **polysepalous**; but when united, **gamosepalous**. In a gamosepalous calyx, the sepals are united below to form a tube, called the **calyx tube**, while the free ends of the sepals are called **calyx lobes** or **teeth**. The number of sepals united is determined by the number of lobes or teeth of the calyx.

The calyx may sometimes be absent in a flower, or modified into a **scaly** structure, as in sunflower (*Helianthus annuus*, Fig. 88, B), and marigold (*Tagetes patula*) of Fam. Compositae, or into a bunch of hair-like structures, called **pappus**, as in *Vernonia cinerea* (Fig. 88, A), *Blumea lacera*, etc., of Fam. Compositae, *Valleriana* sp. (Fam. Vallerianaceae, Fig. 88, F); or **spine**, as in water chestnut (*Trapa bispinosa*, Fig. 88, C) of Fam. Onagraceae; or **spur**, *i.e.*, beak-like structure, as in balsam (*Impatiens balsamina*) of Fam. Balsaminaceae, and garden nasturtium (*Tropaeolum majus*, Fig. 88, D) of Fam. Tropaeolaceae; or **hood**, as in monk's hood (*Aconitum napellus*, Fig. 88, E) of Fam. Ranunculaceae.

Duration of calyx. After the opening of the flower, the calyx usually withers away, but it may persist in some cases. Sometimes, the calyx falls off even before the flowers are fully

open ; such a calyx is said to be **fugacious** or **caducous**, as in poppy (*Papaver somniferum*) and Mexican poppy (*Argemone mexicana*) of Fam. Papaveraceae, *Magnolia grandiflora* (Fam. Magnoliaceae), etc. When it falls off after the opening of the flower, it is said to be **deciduous**, as in lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae. In other cases,

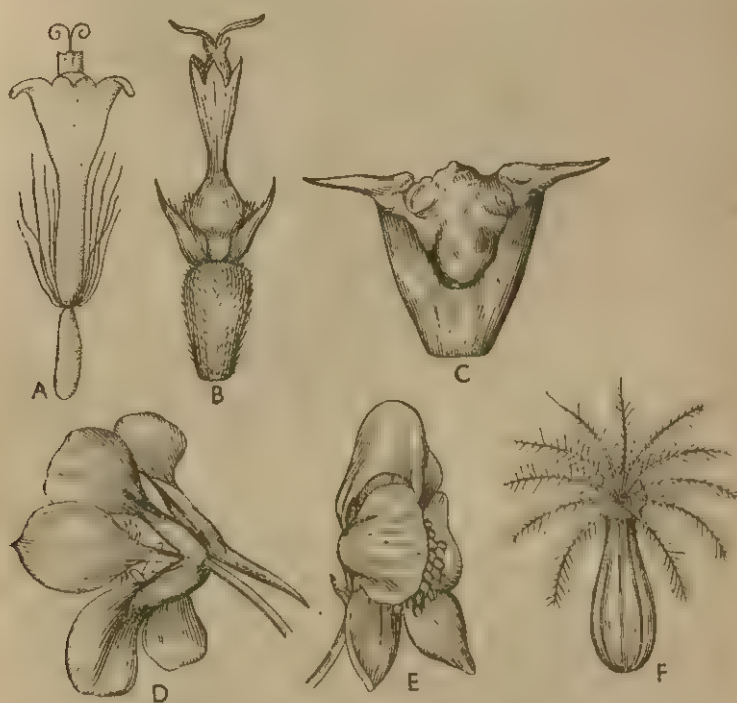


FIG. 88. MODIFICATION OF CALYX

A, pappus of *Vernonia* ; B, scales of *Helianthus* ; C, spine of *Trapa* ; D, spur of *Tropaeolum* ; E, hood of *Aconitum* ; F, pappus of *Valleriana*.

when the calyx persists, it is called **persistent**. A persistent calyx may be either **marcescent**, i.e., persistent but ceases to grow, as in tomato (*Lycopersicum esculentum*) of Fam. Solanaceae, pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae) etc., or **accrescent**, i.e., it not only persists, but also grows along with the development of the fruit, as in brinjal (*Solanum*

melongena) of Fam. Solanaceae, *Dillenia indica* (Fam. Dilleniaceae), etc. ; in the latter case the calyx is fleshy.

Forms of calyx. Regular and polysepalous calyx is found in Fams. Cruciferae (Fig. 89, A), Capparidaceae, Nymphaea-

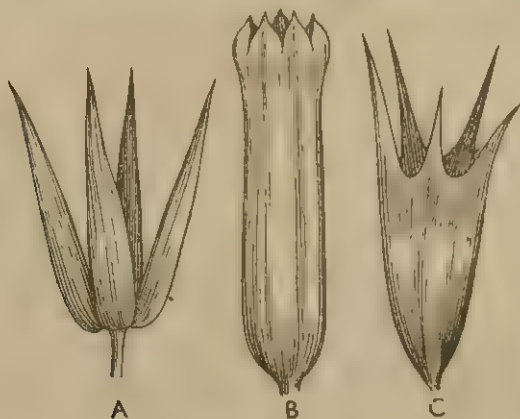


FIG. 89. DIFFERENT FORMS OF CALYX

A, regular and polysepalous in *Barssica* ; B, regular and gamosepalous in *Datura* ; C, irregular and gamosepalous (bilabiate) in *Leonurus*.

ceae, etc. Irregular and polysepalous calyx is found in monk's hood (*Aconitum napellus*) of Fam. Ranunculaceae, where there are five sepals, of which the posterior one is the largest, and of the other four, two form a lateral pair and the remaining two an anterior pair. Regular and gamosepalous calyx is found in Fams. Malvaceae, Solanaceae (Fig. 89, B), Convolvulaceae, etc. Irregular and gamosepalous calyx is found in Fam. Labiatae and some members of Fam. Acanthaceae, where the calyx is **bilabiate** (Fig. 89, C) the upper or posterior lip consisting of three sepals and the lower or anterior one of two sepals. It is to be noted that gamosepalous calyx is found, as a rule, in plants having flowers with a gamopetalous corolla, but the same occurs also in Fams. Malvaceae, Leguminosae, etc., where the petals are distinctly free.

THE COROLLA

The corolla is the second inner and upper accessory floral whorl consisting of **petals**. The petals are usually brightly

coloured*, sweet-scented†, broad, and inserted on the thalamus by a relatively narrow base. Sometimes they become green, and then are said to be **sepaloid** or **sapaline**. as in custard apple (*Anon squamosa*), *Polyalthia longifolia* and *Artabotrys odoratissima* of Fam. Anonaceae, green roses of Fam. Rosaceae, *Pergularia* sp. (Fam. Asclepiadaceae), etc. They are often differentiated into a narrow lower portion, called the **claw**, and an upper expanded portion, the **limb** or **blade**, as in Fams. Cruciferae, Caryophyllaceae, etc. Like leaves, they possess stomata and venation.

Like sepals, the petals not only protect the inner essential sets of floral leaves from sunshine and rain, but also, owing to their large size, conspicuous coloration and sometimes by their sweet scents, attract insects for pollination, which is essential for seed-formation.

Like calyx, the corolla may be **regular** or **irregular**. When all the petals remain free from one another, the corolla is said to be **polypetalous**, but when united, it is said to be **gamopetalous** or **sympetalous**. When gamopetalous, it often forms a lower tubular portion, known as the **corolla tube**, and the upper free portions are the **corolla lobes**. The region, where the tube ends into the lobes, is called the **throat**.

Sometimes appendages develop on the corolla, such as **spurs** or prolonged tube-like structures for storing nectar, as in larkspur (*Delphinium majus*, Fig. 90, A) of Fam. Ranunculaceae, *Ionodium suffruticosum* (Fam. Violaceae), etc.; or **corona**, which is an outgrowth arising from the throat of the corolla tube, or in between the corolla and the androecium in the form of lobes, scales or hairs, as in *Wrightia tomentosa* and oleander (*Nerium odorum*) of Fam. Apocynaceae, passion flower (*Passiflora*

* The colour of the petals may be due either to (a) pigments dissolved in the cell sap, or to (b) pigments in the chromoplasts, or to (c) both. The coloured substance of the cell sap is mainly anthocyanin, which gives red, blue or violet colour to petals. The yellow, orange and red colour of the chromoplasts are due to carotenoids. The whiteness of the petals is due to the reflection of light from numerous air-spaces in the tissue of the petals.

† The scents produced by the petals are due to the essential oils excreted by certain special cells forming glands, called **nectaries**, which are usually situated at the base of the petals on the inner surfaces. Nectaries may also occur elsewhere in the flower.

suberosa, Fig. 90, B) of Fam. Passifloraceae, *Scoparia dulcis* (Fam. Scrophulariaceae), *Daemia extensa* (Fam. Asclepia-



FIG. 90. APPENDAGES OF COROLLA

A, in *Delphinium* ; B, in *Passiflora* ; C, in *Cypripedium* ; D, in *Daemia*.

daceae, Fig. 90, D). *etc.* The corona enhances the beauty of a flower.

The corolla may be actinomorphic, zygomorphic, or asymmetrical. In a zygomorphic corolla, prominent features, such as hood, spur, flag, or platform (**labellum**) develop, which lead to the various degrees of zygomorphy, and, in some cases, irregularity also adds to the beauty and prominence of a flower. Thus, it is an adaptation to attract insects for cross-pollination.

Forms of corolla. The corolla, whether regular or irregular, polypetalous or gamopetalous, is of diverse forms. The principal types are stated below.

(a) *Regular and polypetalous*

Cruciform, when the corolla consists of four-clawed petals arranged at right angles to one another in the form of a Mal-

tese cross, as in mustard (*Brassica nigra*, Fig. 91, A) radish (*Raphanus sativus*) and other plants of Fam. Cruciferae.



FIG. 91. REGULAR POLYPETALOUS COROLLA
A, Cruciform ; B, Caryophyllaceous ; C, Rosaceous.

Caryophyllaceous, when the corolla consists of five clawed petals with spreading limbs, *i.e.*, claws and limbs are at right angles to each other, as in pink (*Dianthus chinensis*, Fig. 91, B), soapwort (*Saponaria vaccaria*) and other plants of Fam. Caryophyllaceae.

Rosaceous, when there are five petals without any claw but with a single anterior odd petal, as in wild rose (*Rosa lucida*, Fig. 91, C) of Fam. Rosaceae, tea (*Cammelia thea*=*Thea sinensis*) of Fam. Theaceae, *etc.*

(b) Irregular and polypetalous

Papilionaceous (Fig. 92), when there are five irregular, free petals suggesting the appearance of a butterfly. The posterior

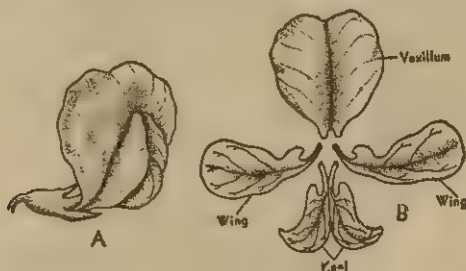


FIG. 92. PAPILIONACEOUS COROLLA

petal is the biggest and outermost, and is called the **vexillum** or **standard**. It includes a pair of lateral petals, known as **alae** or **wings**, which, in their turn, include another pair of smaller lateral petals very slightly united below to form a small boat-

shaped structure, known as the **keel** or **carina**. Common examples are pea (*Pisum sativum*), *Clitoria ternatea*, *Sesbania grandiflora* and other plants of S.F. Papilionaceae (Fam. Leguminosae).

(c) *Regular and gamopetalous*

Tubular, when the corolla tube is more or less cylindrical, as in the disc florets of sunflower (*Helianthus annuus*, Fig. 93, A) and many other plants of Fam. Compositae.

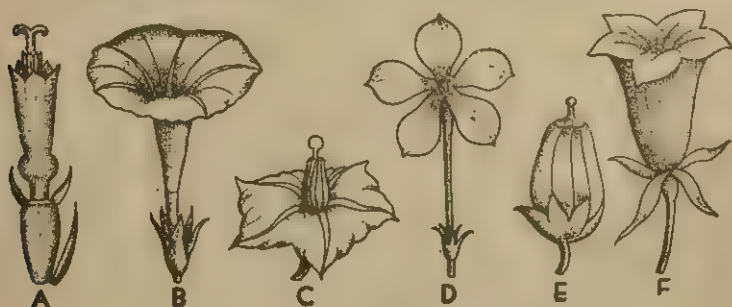


FIG. 93. REGULAR GAMOPETALOUS COROLLA

A, tubular ; B, infundibuliform ; C, rotate ; D, hypocrateriform ; E, urceolate ; F, campanulate.

Campanulate or bell-shaped, when the corolla tube is inflated below and somewhat widened out at the top, as in gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, Cape gooseberry (*Physalis peruviana*, Fig. 93, F) of Fam. Solanaceae, *Thevetia peruviana* (= *T. neriifolia*) of Fam. Apocynaceae, etc.

Infundibuliform or funnel-shaped, when the corolla tube is tubular below and gradually widened out at the top, as in thorn apple (*Datura fastuosa*) of Fam. Solanaceae, morning glory (*Ipomoea pulchella*, Fig. 93, B) of Fam. Convolvulaceae, *Ruellia tuberosa* (Fam. Acanthaceae), etc.

Rotate or wheel-shaped, when the corolla tube is short with spreading limbs at right angles to it, as in brinjal (*Solanum melongena*, Fig. 93, C) and other species of the genus *Solanum* belonging to Fam. Solanaceae, *Nyctanthes arbor-tristis* (Fam. Oleaceae)*, *Hemidesmus indicus*, *Asclepias acida* and *Calotropis procera* of Fam. Asclepiadaceae, *Scoparia dulcis* (Fam. Scrophulariaceae), etc.

* Fam. Verbenaceae, according to Shaw (1952).

Hypocrateriform or salver-shaped, when the corolla tube is comparatively long and narrow with spreading limbs, as in periwinkle (*Vinca rosea*, Fig. 93, D), *Ervatamia indica* (= *Tabernaemontana coronaria*) and some other plants of Fam. Apocynaceae, *Ixora coccinea* (Fam. Rubiaceae), *Ipomoea quamoclit* (Fam. Convolvulaceae), etc.

Urceolate or urn-shaped, when the corolla tube is inflated in the middle but narrow above and below, as in *Bryophyllum calycinum* (Fam. Crassulaceae, Fig. 93, E) *Rhododendron* sp. (Fam. Ericaceae), etc.

(d) *Irregular and gamopetalous*

Ligulate or strap-shaped, when the corolla tube is short and tubular at the base but flat above like a strap, as in the ray florets of sunflower (*Helianthus annuus*, Fig. 94, A) and a few other plants of Fam. Compositae.

Bilabiate or two-lipped, when the limb of the corolla is divided into two portions or lips, the upper and the lower, with the mouth remaining wide open, as in *Leonurus sibiricus*, *Ocimum sanctum*, *Anisomeles ovata*, *Leucas aspera* (Fig. 94, B) and other plants of Fam. Labiatae, *Hygrophila spinosa*, *Adhatoda vasica*, *Diclip-*



FIG. 94. IRREGULAR GAMOPETALOUS COROLLA
A, ligulate ; B, bilabiate ; C & D, personate.

tera roxburghii, *Peristrophe bicalyculata*, *Andrographis paniculata*, *Cardenthera triflora*, *Hemigraphis hirta* and a few other plants of Fam. Acanthaceae. It is to be noted that usually the upper or posterior lip is composed of two petals and the lower or anterior one, of three petals. But, in sacred basil (*Ocimum sanctum*) of Fam. Labiatae, the upper lip consists of one petal and the lower lip, of four petals.

Personate or masked, when the limb of the corolla is two-lipped as in the previous case, but the mouth remains closed by a projection, known as the **palate**, from the lower lip, as in *Lin-denbergia indica* (= *L. urticaefolia*), snapdragon (*Antirrhinum majus*, Fig. 94, C) toad flax (*Linaria ramosissima*, Fig. 94, D)* and a few other plants of Fam. Scrophulariaceae.

AESTIVATION OR PREFLORATION (Fig. 95)

The aestivation is the mode of arrangement of sepals or petals with respect to one another in the bud state. It is of the following types :

Valvate, when the margins of the sepals or the petals either touch or lie very close to one another without any overlapping, as in custard apple (*Anona squamosa*) and other plants of Fam. Anonaceae, mustard (*Brassica nigra*) of Fam. Cruciferae, sensitive plant (*Mimosa pudica*), gum tree (*Acacia arabica*) and other plants of S.F. Mimosae (Fam. Leguminosae), petals of *Calotropis procera* (Fam. Asclepiadaceae), etc.

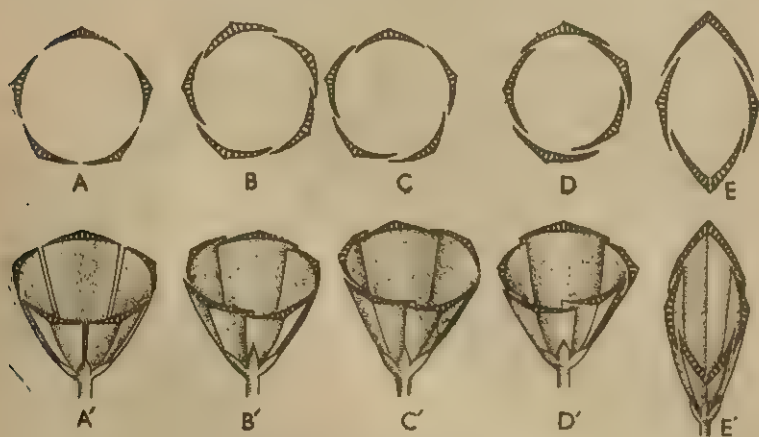


FIG. 95. AESTIVATION (Diagrammatic)

A-A', valvate ; B-B', imbricate ; C-C', twisted ; D-D', quincuncial ;
E-E', vexillary.

* The personate corolla of toad flax is spurred at the base, and is also known as saccate.

Twisted or **contorted**, when the margins of the sepals or the petals are overlapping along one margin but overlapped along the other in regular succession, as in cotton (*Gossypium herbaceum*), China rose (*Hibiscus rosa-sinensis*) and some other plants of Fam. Malvaceae, thorn apple (*Datura fastuosa*) and some plants of Fam. Solanaceae, oleander (*Nerium odorum*), *Thevetia peruviana* (= *T. nerifolia*) and other plants of Fam. Apocynaceae, etc.

Imbricate, when the margins of the sepals or the petals are arranged in such a manner that one is external (i.e., its both margins are overlapping, one is internal (i.e., its both margins are overlapped), and others are overlapping along one margin but overlapped along the other, as in poppy (*Papaver somniferum*) of Fam. Papaveraceae, rose (*Rosa centifolia*) of Fam. Rosaceae, *Cassia fistula*, *Caesalpinia pulcherrima* and other plants of S.F. Caesalpinieae (Fam. Leguminosae), etc.

Quincuncial, when the margins of the sepals or the petals are arranged in such a manner that two of them are external, two internal, and the remaining one is overlapping along one margin but overlapped along the other, as in sepals of *Calotropis procera* (Fam. Asclepiadaceae), *Ipomoea reptans* (Fam. Convolvulaceae), guava (*Psidium guayava*) of Fam. Myrtaceae, etc.

Vexillary, when of the five petals the posterior odd petal is the largest and covers the two lateral petals, which, in their turn, overlap two other smaller lateral ones, as in the papilionaceous corolla. It is only found in the S.F. Papilionaceae (Fam. Leguminosae).

THE ANDROECIUM

The androecium is the third inner and upper set of floral members. It is composed of *stamens* or *microsporophylls*, which are very different in appearance from both the sepals and petals, and may be either indefinite or definite, ranging from many to one in number. These may or may not bear any relation to the number of sepals, petals and carpels*. According to the number of stamens, the flower may be

* When the number of stamens in a flower equals that of the sepals, petals and carpels, the androecium is said to be *isostemonous*.

monandrous, when there is only one stamen, as in ginger (*Zingiber officinale*), turmeric (*Curcuma longa*) and other plants of Fam. Zingiberaceae ; **diandrous**, when there are two stamens, as in *Adhatoda vasica* (Fam. Acanthaceae), jasmine (*Jasminum* sp.) and other plants of Fam. Oleaceae, etc. ; **triandrous**, when there are three stamens, as in wheat (*Triticum aestivum* = *T. vulgare*) and many plants of Fam. Gramineae, sedges (Fam. Cyperaceae), etc. ; **tetrandrous**, when there are four stamens, as in sacred basil (*Ocimum sanctum*) and some other plants of Fam. Labiatae, *Scoparia dulcis* (Fam. Scrophulariaceae), *Ixora* sp. (Fam. Rubiaceae), etc. ; **pentandrous**, when there are five stamens, as in thorn apple (*Datura fastuosa*) and other plants of Fam. Solanaceae, *Ipomoea* sp. and other members of Fam. Convolvulaceae, etc. ; **hexandrous**, when there are six stamens, as in paddy (*Oryza sativa*) and bamboo (*Bambusa arundinacea*) of Fam. Gramineae, and so on. When numerous stamens are present in a flower, as in rose (*Rosa centifolia*) of Fam. Rosaceae, it is said to be **polyandrous**. The androecium is regarded as one of the essential sets of the flower, and is concerned with the sexual reproduction of the plant. The stamens may be arranged on the receptacle in *spirals* (e.g., members belonging to Fams. Magnoliaceae, Anonaceae, Nymphaeaceae, etc.), *whorls* (e.g., members of Fams. Caryophyllaceae, Geraniaceae, Rutaceae, etc.), or *fascicles* (clusters), as met with in the members of Fams. Cactaceae, Dilleniaceae, etc.

PARTS OF A STAMEN (Fig. 96). Each stamen normally consists of a more or less slender stalk or **filament** bearing at its apex a somewhat cylindrical or knob-like head, called the **anther**. A primitive stamen, as is found in some woody members of the Order Ranales, however, cannot be differentiated into filament and anther. The anther generally consists of two longitudinal halves or lobes, and, is termed as **ditheous** ; but, in some cases, as in Fam. Malvaceae, it is with one lobe only, and is called **monotheous**. The lobes are usually united by a band of tissue, called the **connective**. Each anther lobe normally contains two longitudinal cavities, called **pollen sacs** or **microsporangia**, containing powdery mass of cells, known as the **pollen grains** or **microspores**, in abundance. At maturity, the intervening wall between two pollen sacs breaks down, so that the two cavities

in each half of the anther lobe become one. The pollen grains, when mature, are ultimately liberated from the anthers. Only

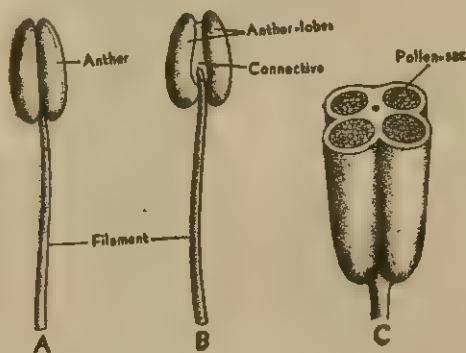


FIG. 96. PARTS OF A STAMEN
A, front view ; B, back view ; C, t.s. of anther.

the fertile stamens can produce pollen grains. On the other hand, the sterile and vestigial stamens, called the **staminodia**, cannot do so. The staminodia are found in a number of families of angiosperms.

THE FILAMENT

The filament is usually slender and thread-like. It may be compared to the stalk of a leaf, but it is not an essential part of the stamen. The length, colour and duration of filaments are very variable, and depending on the nature of the filaments, stamens may be erect, incurved, recurved or pendulous, etc. When the filament is absent, the stamen is **sessile**. The main function of the filament is to support the anther, which is the essential part in spore production.

The filament may be **flat and leaf-like**, as in water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae, or **club-shaped** with ear-like base, as in bay (*Cinnamomum tamala*), camphor (*Cinnamomum camphora*) and other plants of Fam. Lauraceae (Fig. 97, E). The filament is usually unbranched, exceptions being found in some cases, as in castor (*Ricinus communis*, Fig. 97, A) of Fam. Euphorbiaceae. When the filament does not bear any anther, it is said to be sterile, and is known as the **staminode** (**staminodium**), as in *Pterospermum acerifolium* (Fam. Sterculia-

ceae), *Mimusops elengi* (Fam. Sapotaceae), etc. Often the staminodia have the forms of petals and are brightly coloured, and these are said to be **petaloid staminodia**, as in Indian shot (*Canna indica*, Fig. 97, C) of Fam. Cannaceae, ginger

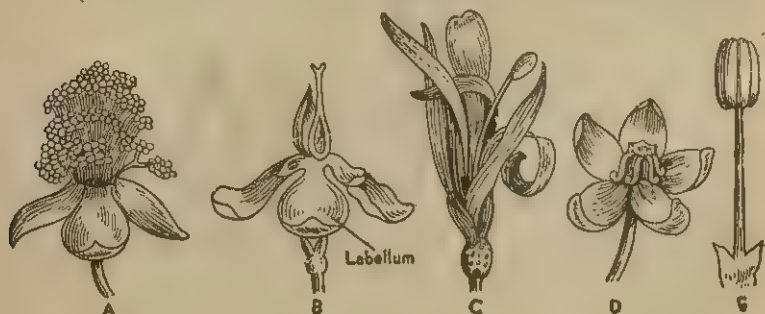


FIG. 97. MODIFIED FILAMENTS

A, branched filament of castor ; B, labellum of ginger ; C, same of *Canna* ; D, staminal corona of *Calotropis* ; E, filament of *Cinnamomum*.

(*Zingiber officinale*, Fig. 97, B) and *Koempferia rotunda* of Fam. Zingiberaceae, all belonging to the Order Scitamineae. It is to be noted that in Fam. Cannaceae, one of the staminodia is the largest forming the **labellum** or landing stage of the insects, but in Fam. Zingiberaceae, two staminodia are united to form the structure. Sometimes, outgrowths, known as **staminal corona**, develop from the filaments, as in *Calotropis procera* (Fam. Asclepiadaceae, Fig. 97, D), *Pancratium verecundum* (Fam. Amaryllidaceae), etc. In the former case, the corona is horn-like, but in the latter, cup-like.

THE CONNECTIVE

The connective is the strip of sterile tissue connecting the two anther lobes of the stamens, and it is in this region that vascular strands are present, which carry food substances to the anther lobes and the pollen grains. It is said to be **discrete**, when the tissue of the connective is narrow, so that the two anther lobes lie close to each other, as in *Adhatoda vasica* (Fam. Acanthaceae, Fig. 98, A) ; **divaricate**, when the tissue of the connective is broad, so that the two anther lobes are separated, as in *Justicia gendarussa* (Fam. Acanthaceae, Fig. 98, B), pansy (*Viola tricolor*) of Fam. Violaceae, *Calamintha* sp.

(Fam. Labiatae) etc. In *Salvia plebeja* (Fam. Labiatae, Fig. 98, C), it may be **elongated and filiform**, so that the two anther lobes are widely separated from each other, the lower

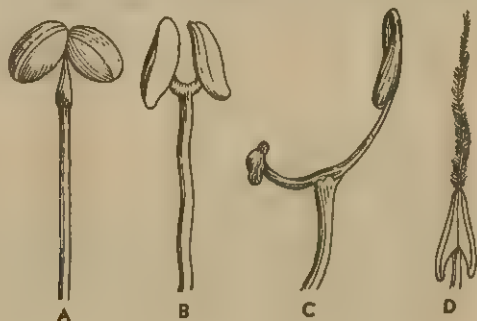


FIG. 98. DIFFERENT TYPES OF CONNECTIVE
A, discrete ; B, divaricate ; C, same of *Salvia* ; D, prolonged.

one being sterile. In oleander (*Nerium odorum*, Fig. 98, D) and some other plants of Fam. Apocynaceae, the connective is **prolonged** beyond the anther, and may bear feathery outgrowths at its apex.

THE ANTHR

As already stated, the anther is the essential part of the stamen, and is situated at the top of the filament. The anther is usually greenish while young, but yellow when fully matured ; it is golden-coloured in *Mesua ferrea* (Fam. Guttiferæ), and red in mignonette (*Reseda odorata*) of Fam. Resedaceæ. In cotton (*Gossypium herbaceum*) and other plants of Fam. Malvaceæ, the anther is one-lobed, and possesses only two pollen sacs. In *Canna indica* of Fam. Cannaceæ, one half of the stamen is fertile, while the other half is sterile and petaloid. The side of the anther to which the connective is attached is called the **back**, and the other side is the **face**.

Attachment of anther

From the morphological standpoint of view, as both an anther and a filament form different parts of the same organ, there can be no question of 'attachment' of one with the other. A stamen, however, is conventionally termed as **basifixed**, when the filament appears to be attached directly at

the base of the anther, as in mustard (*Brassica nigra*, Fig. 99, A) of Fam. Cruciferae, sedges (Fam. Cyperaceae), etc. ; **dorsifixed**, when the filament appears to be attached to the back or the broad side of the anther, as in water lily (*Nymphaea stellata*, Fig. 99, B) of Fam. Nymphaeaceae, *Magnolia grandiflora* (Fam. Magnoliaceae, Fig. 99, C), tuberose (*Polianthes tuberosa*, Fig. 99, D)

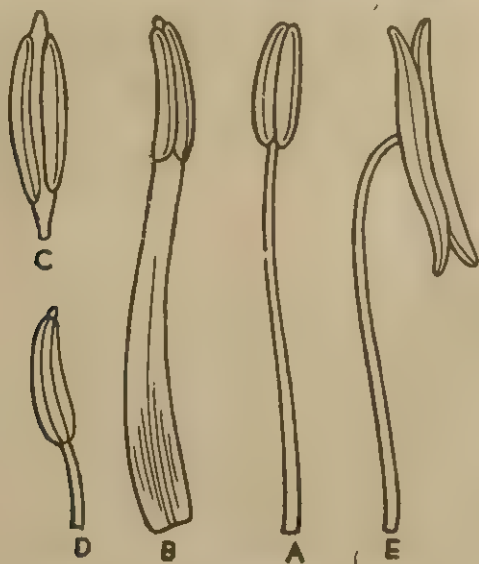


FIG. 99. ATTACHMENT OF ANTHER

A, basifixed anther of mustard ; B, dorsifixed anther of water lily ; C, same of *Magnolia* ; D, same of tuberose ; E, versatile anther of wheat.

of Fam. Amaryllidaceae, etc. ; and **versatile**, when the filament is 'attached' to a point at about the middle of the back of the connective, so that the anther swings freely upon it, as in wheat (*Triticum aestivum*=*T. vulgare*, Fig. 99, E) and other members of Fam. Gramineae, glory lily (*Gloriosa superba*) of Fam. Liliaceae, spider lily (*Crinum asiaticum*) of Fam. Amaryllidaceae, etc. Of these three types, the first one is considered to be the most primitive.

Forms of anther lobes

The anther lobes are also of various forms. These may be **linear**, as in *Acalypha* sp. (Fam. Euphorbiaceae, Fig. 100, D),

water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae, etc. ; **oval**, in almond (*Prunus amygdalis*) of Fam. Rosaceae; **ellipsoid** or like an ellipse, as in brinjal (*Solanum melongena*) of Fam. Solanaceae; **rectangular** or four-sided, as in *Solanum* sp. (Fam. Solanaceae); **reniform** or kidney-shaped, as in China rose (*Hibiscus rosa-sinensis*, Fig. 100, B) and other plants of Fam.

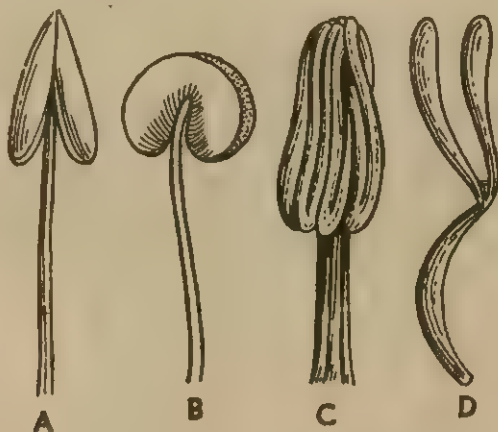


FIG. 100. FORMS OF ANTHER-LOBES
A, sagittate ; B, reniform ; C, sinuous ; D, linear.

Malvaceae; **sagittate** or arrow-shaped, as in periwinkle (*Vinca rosea*, Fig. 100, A) and some other plants of Fam. Apocynaceae ; **sinuous** or peculiarly rolled up in the form of inverted 'S', as in gourd (*Cucurbita maxima*, Fig. 100, C) and other plants of Fam. Cucurbitaceae ; **cordate** or heart-shaped, as in *Atalantia monophylla* (Fam. Rutaceae).

Dehiscence of anther lobes (Fig. 101)

When the anthers become mature, the pollen grains within the pollen sacs exert some pressure on the outer wall, as a result of which, the anther lobes usually burst open and the pollen grains are set free. The following are the four main kinds of dehiscence : **longitudinal**, when the anther lobes split up lengthwise, as in custard apple (*Anona squamosa*) of Fam. Anonaceae, thorn apple (*Datura fastuosa*) of Fam. Solanaceae, etc. ; **transverse**, when the anther lobes split up crosswise, as in

duck weed (*Lemna trisulca*) of Fam. Lemnaceae, *Alchemilla* sp. (Fam. Rosaceae), etc. ; **valvular**, when the anther lobes open on the outer side only by small flaps or valves, as in berberry (*Berberis asiatica*) and other plants of Fam. Berberidaceae, cinnamon (*Cinnamomum zeylanicum*) and other plants of Fam. Lauraceae; **porous***, when the anther lobes open by small holes or pores at their apices, as in potato (*Solanum tuberosum*) and many other plants of Fam. Solanaceae. Basing on the direction of dehiscence of the anther lobes, it (dehiscence) may be primarily differentiated into two types, **introrse** and **extrorse**. In the former case, the pollen grains are discharged directly or

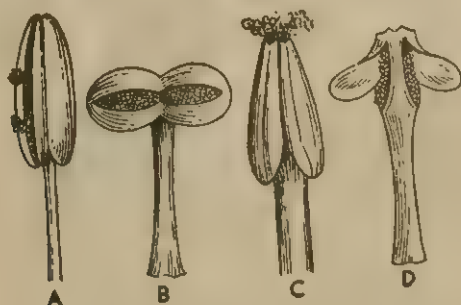


FIG. 101. DEHISCENCE OF ANTHER LOBES

A, longitudinal ; B, transverse ; C, porous ; D, valvular.

somewhat obliquely towards the interior of the flower, while, in the latter, towards the exterior. The introrse type of dehiscence is characteristic of the majority of angiospermic flowers, the extrorse type being found in a few families only, like Cucurbitaceae, Aristolochiaceae, Iridaceae, Potamogetonaceae, and others. Some families, like Magnoliaceae, Alismataceae, Liliaceae, etc., are characterized by having both the types in their different genera. Of the two whorls of stamens in *Fagopyrum* (Fam. Polygonaceae), one is introrse, the other extrorse. In *Cinnamomum* (Fam. Lauraceae) with a polystemonous androecium, two whorls of stamens are introrse, and one extrorse, while of the three stamens in *Commelina* (Fam. Commelinaceae), two are extrorse, and one introrse. Besides the two types of dehiscence

* Strictly speaking, it is not a case of dehiscence, since the anther lobes do not burst out fully.

referred to above, there is a third one, which is termed as **latrorse**, when the pollens are discharged laterally, as is found in the Fams. Ranunculaceae, Menispermaceae, Butomaceae, as well as in some genera belonging to the Fams. Primulaceae, Solanaceae, Valerianaceae, etc.

Whorls of stamens

Usually, there is only one whorl of stamens, which generally alternate with the petals. Sometimes, two or more whorls of stamens are present, and these, as a rule, alternate with each other, but may alternate with the petals or lie opposite to them. Thus, the androecium is said to be **haplostemonous**, when there is one whorl of stamens, which usually alternate with the petals, as in morning glory (*Ipomoea pulchella*) and other plants of Fam. Convolvulaceae; **diplostemonous**, when there are two whorls of stamens, of which the outer whorl alternates with the petals, and the inner one lies opposite to them, as in pink (*Dianthus chinensis*) and other plants of Fam. Caryophyllaceae, Mexican poppy (*Argemone mexicana*) and other plants of Fam. Papaveraceae, etc.; **obdiplostemonous**, when there are two whorls of stamens, of which the outer whorl lies opposite to the petals and the inner one alternates with them, as in lemon (*Citrus limon*) and other plants of Fam. Rutaceae; and **polystemonous**, when the stamens occur in more than two whorls, as in *Delphinium* sp. (Fam. Ranunculaceae), members of Fam. Lauraceae, etc. Stamens are said to be **antipetalous**, when there is one whorl of stamens, which lie opposite to the petals, as in jujube (*Zizyphus jujuba*) and other plants of Fam. Rhamnaceae, *Portulaca oleracea* and other plants of Fam. Portulacaceae, wood sorrel (*Oxalis corniculata*) and other plants of Fam. Oxalidaceae, *Vitis* sp. and other plants of Fam. Vitaceae, etc.

Insertion of stamens. According to the position of stamens with reference to the ovary, these may be *hypogynous*, *perigynous* and *epigynous*, as already described before.

Relative lengths of stamens

The relative lengths of stamens with respect to one another may be of two types : **didynamous**, when there are four stamens

in a flower, of which two are long and two short, as in sacred basil (*Ocimum sanctum*), *Leonurus sibiricus* and other plants of Fam. Labiatae, *Lindenbergia indica* (= *L. urticaefolia*, Fig. 102, B), *Antirrhinum majus* and the majority of plants of Fam. Scrophulariaceae, *Hygrophila spinosa*, *Andrographis paniculata* and a few other plants of Fam. Acanthaceae, *Lantana camara*, teak (*Tectona grandis*) and many other plants of Fam. Verbenaceae,

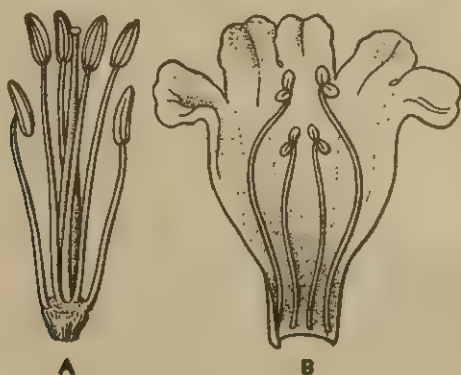


FIG. 102. RELATIVE LENGTHS OF STAMENS
A, tetradynamous ; B, didynamous.

etc. ; and **tetradynamous**, when, out of six stamens, four are long and two short, as in mustard (*Brassica nigra*, Fig. 102, A), radish (*Raphanus sativus*) and other plants of Fam. Cruciferae.

When the relative lengths of the stamens are considered with regard to the corolla, two conditions are met with : **inserted**, when the stamens are shorter than the corolla, and **exserted**, when they are longer, as in sensitive plant (*Mimosa pudica*), gum tree (*Acacia arabica*), and other plants of S.F. Mimosae (Fam. Leguminosae), spider flower (*Gynandropsis gynandra* = *G. pentaphylla*), *Capparis sepiaria*, and a few other plants of Fam. Capparidaceae, *Clerodendrum petasites* (= *Clerodendron infortunatum*) of Fam. Verbenaceae, *etc.*

Union of stamens

The union of stamens takes place either amongst themselves or with other whorls. In the former case, it is known

as *cohesion* or *connation**, and, in the latter, *adhesion* or *adnation*.

The **cohesion of stamens** (Fig. 103) is of the following kinds : When union takes place between the anthers, the filaments remaining free, the androecium is said to be **syngenesious** or **synantherous**, as in sunflower (*Helianthus annuus*, Fig. 103, D),

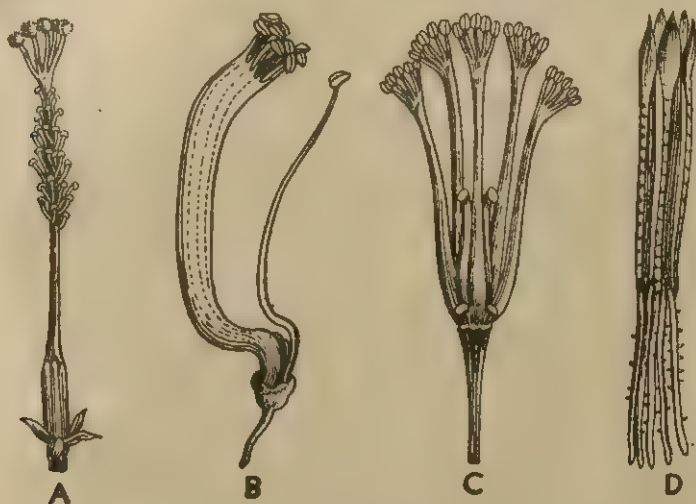


FIG. 103. COHESION OF STAMENS

A, monadelphous ; B, diadelphous ; C, polyadelphous ; D, syngenesious.

marigold (*Tagetes patula*), and other plants of Fam. Compositae, gourd (*Cucurbita maxima*), and other plants of Fam. Cucurbitaceae. According to the number of bundles formed due to cohesion of filaments, the androecium may be : **monadelphous**, as in cotton (*Gossypium herbaceum*), China rose (*Hibiscus rosa-sinensis*, Fig. 103, A) and other plants of Fam. Malvaceae ; **diadelphous**, as in pea (*Pisum sativum*, Fig. 103, B), *Sesbania grandiflora* and other plants of S.F. Papilionaceae (Fam. Leguminosae) excepting *Crotalaria*, where it is monadelphous ; and **polyadelphous**,

* Strictly speaking, **cohesion** means a somewhat loose type of union among similar members, while **connation** signifies such a union having histological significance, where the lines of union may be obliterated, or may remain distinct. From this standpoint, the anthers in Fam. Compositae are coherent, while those in Fam. Cucurbitaceae are connate.

as in silk cotton (*Salmaalial malabaricum* = *Bombax malabaricum*) of Fam. Bombacaceae, orange (*Citrus sinensis* = *C. aurantium*, Fig. 103, C), Chinese box (*Murraya paniculata* = *M. exotica*) and some other plants of Fam. Rutaceae, etc. When there is no cohesion among the stamens, the androecium is said to be **adelphous**.

The **adhesion of stamens** to other floral organs varies considerably in extent, and the evidence of such an adnation may remain external, or may be purely internal. The stamens are commonly united with the petals, giving rise to the **epipetalous** condition, as is found in most of the gamopetalous flowers (exceptions being noted in Fams. Campanulaceae and Ericaceae), and rarely with the sepals (**episepalous**), as in Fam. Proteaceae. When united with the perianth leaves, the stamens are said to be **epiphyllous**, as in tuberose (*Polianthes tuberosa*), spider lily (*Crinum asiaticum*) and other plants of Fam. Amaryllidaceae. A **gynostemium*** is formed, when adhesion takes place between stamens and styles as well as stigmas, as is found in the members of Fams. Stylidiaceae, Aristolochiaceae, Asclepiadaceae, and Orchidaceae.

FORMATION AND STRUCTURE OF POLLEN GRAINS OR MICRO-SPORES (Figs. 104—106).

The stamen primordium develops on the receptacle (of the flower) in the form of a semi-lunar projection. On making a cross section of a very young anther, in the early stage of its development in the primordium, masses of cells with larger size, denser cytoplasmic contents, and larger nuclei will be noted in the centre of each of its four angles (Fig. 104, A). These cells constitute the **archesporium**. The archesporial cells become enlarged in the radial direction and divide periclinally, forming two layers of cells. The outer layer is called the **tapetum** (a nutritive tissue, supplying food to the developing pollen grains), while the inner one forms the layer of **primary sporogenous cells**. The tissues lying outside the archesporium give rise to the anther wall, which consists, usually, of three different zones in succession (from outside inwards), namely, the single-layered **epidermis**, the solitary **fibrous**

* Also termed as gynostegium.

layer,* and one or more **parietal** or **wall layers**. The primary sporogenous cells may either behave directly as **pollen mother-cells (microspore mother-cells)**, or may divide giving rise to daughter cells, which then act as spore mother-cells. In case where the primary sporogenous cells undergo divisions, the tapetal cells may also divide forming a tapetal sheath. Each pollen

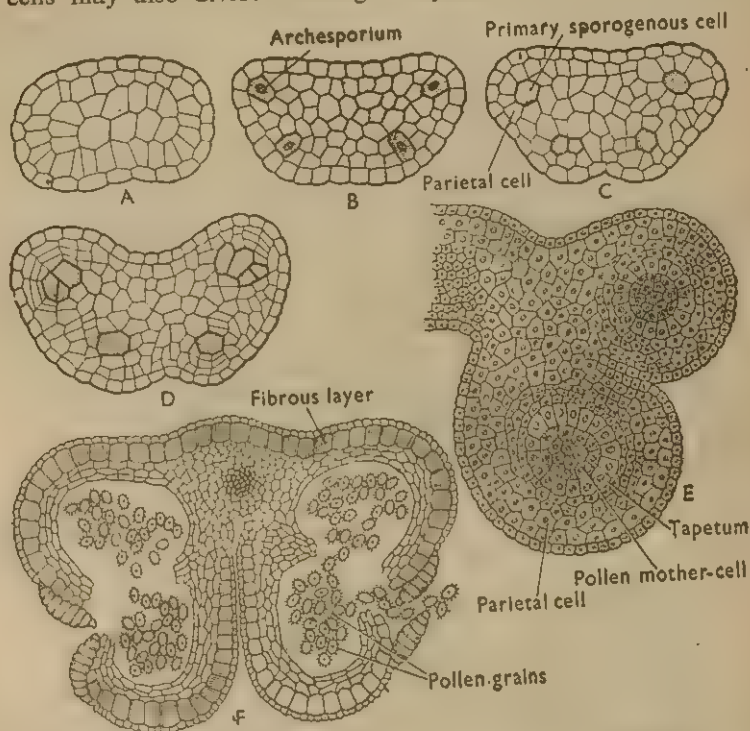


FIG. 104. A-F, STAGES IN THE DEVELOPMENT OF ANTHER AND POLLEN GRAINS.

mother-cell divides meiotically and usually produces four **pollen grains (microspores)**. In some cases, the number of pollen grains produced from each pollen mother-cell may be more than four (**polyspory**) or less, due to irregular or incomplete divisions. With advancement in age, the walls of the cells of the fibrous layer become lignified or suberized with thin original cellulosic walls here and there. As a result of drying, these thick and thin

* In anthers having valvular or porous dehiscence, the fibrous layer is usually either not developed at all, or developed very feebly.

areas on the walls undergo unequal shrinkage, causing the anther wall to get ruptured. Consequently, the pollen grains are liberated.

The pollen grains are asexual reproductive units. They look like yellow particles of dust and have various forms,

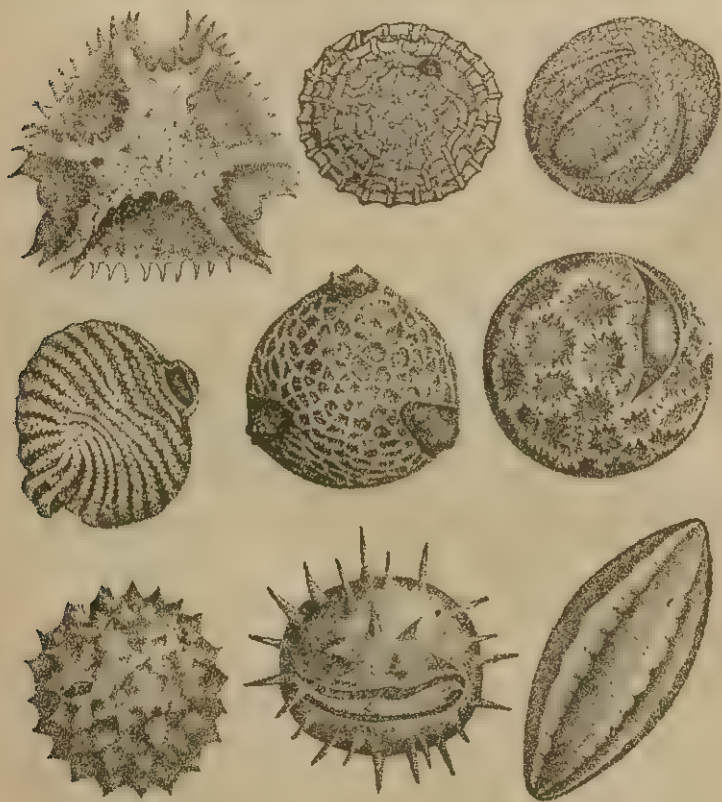


FIG. 105. DIFFERENT KINDS OF POLLEN GRAINS

and shapes (Fig. 105), the commonest being *spherical* or *oval*. Sometimes these may be *polyhedral*, as in milk thistle (*Sonchus palustris*) of Fam. Compositae, *trigonal*, i.e., triangular with rounded and enlarged angles, as in plants commonly belonging to Fam. Onagraceae, *cubical*, as in *Basella alba* (Fam. Basellaceae), or *cylindrical*, as in *Rheo discolor* (Fam. Commelinaceae). In size, they usually vary

from about 1/200—1/1,000 of an inch in diameter, but this is also liable to variation. Each pollen grain is unicellular and usually provided with two coats.* The outer coat, called the **exine** or **extine**, is cuticularized, while the inner coat, the **intine**, is thin. The exine is differentiable into two regions, the outer one of which is known as the **sexine**, while the inner one is called the

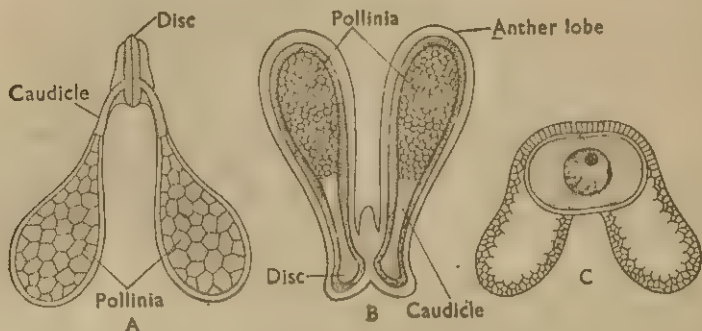


FIG. 106. POLLEN GRAINS AND POLLINIA

A, pollinia of *Calotropis*. B, same of *Orchis*; C, pollen of *Pinus*.

nexine, which appears as a continuous dark-coloured ring under the microscope. The **sexine** may be smooth, spinous, tuberculated or variously sculptured, and may often be provided with distinct ridges and furrows. Small circular pits, called the **germ pores**, are left at places as unthickened areas on the **sexine**. There may be one or more germ pores on each pollen grain, and through these the intine emerges out in the form of tubes (**pollen tubes**) during germination. The cavity inside the intine is filled up with protoplasm containing a well-differentiated nucleus. Usually at maturity, the four cells of a **pollen tetrad**, produced as a result of the reduction division of the pollen mother-cell, separate from one another. But in bulrush (*Typha angustata*) of Fam. Typhaceae and some other plants, these do not separate. In *Calotropis procera* (Fig. 106, A) and many other plants of Fam. Asclepiadaceae, as well as in the orchids of Fam. Orchidaceae (Fig. 106, B), all the grains within each pollen sac are united into a mass,

* Pollens of members of Fam. Najadaceae possess only a single unculticularized coating.

forming the **pollinium**. The pollinia are usually found in pairs. The pollen grains of pine (Fig. 106, C), are provided with two winged expansions from the exine (*winged pollens*), and these help in the dispersal by wind.

THE GYNAECIUM

The stamens are succeeded by one or more **carpels** or **megasporophylls**, which collectively form the **gynaecium** or **pistil**, representing another essential set of floral members.

When there is only one carpel in the gynaecium, it is said to be **simple** or **monocarpellary**, as in the Fams. Leguminosae, Nyctaginaceae, *etc.* In the majority of cases, however, the gynaecium is **compound** or **multicarpellary**, as it consists of more than one carpels. Thus, it is **bicarpellary** in Fams. Cruciferae, Compositae, Solanaceae, *etc.* ; **tricarpellary** in Fams. Cucurbitaceae, Liliaceae, *etc.* ; and **polycarpellary** in Fams. Anonaceae, Malvaceae, *etc.* In such cases, either the carpels are all free, or these may be united with one another. The former case is known as **apocarpy**, as found in Fams. Magnoliaceae (Fig. 107, B) Ranunculaceae, Anonaceae, Alismataceae, rose (*Rosa centifolia*) of Fam. Rosaceae, lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae, *etc.* ; and the latter **syncarpy**, as in Fams. Compositae, Cruciferae, Solanaceae, Cucurbitaceae, Liliaceae, *etc.* Such gynaecia are known as *apocarpous* and *syncarpous* respectively.

Parts of a carpel

Like stamens, carpels also may be either simple or complex. In a simple type of carpel (Fig. 107, A), which is illustrated by some of the woody Ranales, there is usually no differentiation into stigma, style and ovary. The pollens, in general, are received on a **stigmatic crest**, developed from papillate surfaces on the margins of the carpellary leaf, which close to form an ovule-containing chamber. Each complex carpel, on the other hand, consists of three parts (Fig. 107, B & C) : the **stigma**, the distal terminal portion of the carpel, the **style**, the slender stalk supporting the stigma, and the **ovary**, the swollen basal region.

THE STIGMA

The stigma is the terminal portion of the carpel and is the receptive surface for the pollen grains. In primitive carpels, the stigma cannot be well differentiated from the style or the ovary, but in the advanced ones, it is usually very distinct. When mature, it secretes a sticky stigmatic fluid for catching the pollen grains. In some cases, as in lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae, *Artabotrys odoratissima* (Fam. Anonaceae), poppy (*Papaver somniferum*) of Fam. Papaveraceae, etc., the style is absent and the stigma is directly situated on the top of the ovary; it is then said to be **sessile**. In a syncarpous pistil, the stigma is said to be **bifid** (Fig. 108, A), when there are two thin strap-shaped structures, as in Fam. Compositae; **trifid**, when there are three strap-shaped structures, as in Fam. Cyperaceae;

bilobed or **bilobate** (Fig. 108, C), when there are two thick parts, as in Fam. Convolvulaceae; **trilobed** or **trilobate**, when there are three thick parts, as in Fam. Cucurbitaceae; **capitate** (Fig. 108, F), when the stigmas are united to form a compound undifferentiated structure, as in Fam. Cruciferae; **laciniate**, when the stigma is fringed, i.e., cut into narrow lobes of equal lengths, as in *Rumex maritimus* (Fam. Polygonaceae); **feathery** (Fig. 108, E), when it has a feathery appearance, as in Fam. Gramineae; **striate** or **radiate** (Fig. 108, G), when there are distinct rays of the stigma in the form of a star, as in Fam. Papaveraceae; and **dumb-bell-shaped**, when it is like a dumb-bell, as in some members of Fam. Apocyanaceae.

In some members of Fam. Orchidaceae, a portion of the stigma is projected, and though itself functionless, it bends over

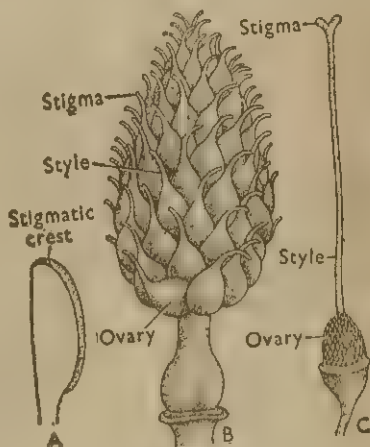


FIG. 107. TYPES OF CARPEL

A, Stigmatic crest in *Drimys* ;
 B, Apocarpous gynaecium of
Michelia ; C, Syncarpous
 gynaecium of *Datura*.

and conceals the receptive portion of the stigmatic surface ; this is known as the **rostellum**.



FIG. 108. FORMS OF STIGMA

A, bifid ; B, pentafid ; C, bilobed ; D, pentalobed ; E, feathery ; F, capitate ; G, striate.

THE STYLE

The style is the portion of the pistil connecting the stigma with the ovary. In many flowers the style is distinct, and may be long or short, or totally absent. It is usually smooth

but sometimes becomes hairy, as in *Naravelia zeylanica* (Fam. Ranunculaceae). The style is usually deciduous, i.e., it dries and falls off soon after pollination, but in many cases, it may be persistent, as in *Naravella zeylanica*, and *Clematis gouriana* of Fam. Ranunculaceae. Sometimes, the style may be leafy and petaloid, as in Indian shot (*Canna indica*) of

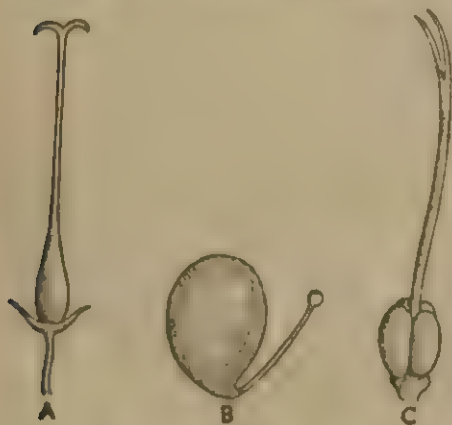


FIG. 109. POSITION OF STYLE

A, terminal ; B, lateral ; C, gynobasic.

Fam. Cannaceae, *Iris nepalensis* (Fam. Iridaceae). etc. The posi-

tion of style may be **terminal**, when it arises from the top of the ovary, as in brinjal (*Solanum melongena*, Fig. 109, A) of Fam. Solanaceae, *Ipomoea* sp. (Fam. Convolvulaceae), etc., **lateral**, when it arises from one side of the ovary, as in mango (*Mangifera indica*, Fig. 109, B) of Fam. Anacardiaceae, members belonging to the sub-families Potentilleae and Chrysobalanioideae of Fam. Rosaceae, etc., and **gynobasic***, when it appears to arise from the base of the 4-lobed ovary or directly from the thalamus, as in members of Fam. Labiatae, *Cynoglossum indicum* (Fig. 109, C) of Fam. Boraginaceae, etc.

In anise (*Foeniculum vulgare*), coriander (*Coriandrum sativum*), and other plants of Fam. Umbelliferae, the base of the style is swollen, and is known as the **stylopodium**.

THE OVARY

The ovary. The ovary is the swollen basal portion of the carpel. When the gynaecium is multicarpellary and apocarpous, as in *Artabotrys odoratissima* (Fam. Anonaceae), *Naravalia zeylanica* (Fam. Ranunculaceae), etc., each carpel forms its separate ovary, style and stigma, so that one gets an aggregation of separate ovaries in such gynaecia. In lotus (*Nelumbium* ~~*Nelumbium*~~ *speciosum*) of Fam. Nymphaeaceae the gynaecium is not only compound and apocarpous, but also the carpels are irregularly embedded in a top-shaped thalamus without any organic union between the tissues of the carpels and the thalamus. On the other hand, when the gynaecium is multicarpellary and syncarpous, all the carpels are usually united to form a single ovary, style and stigma.† But in some cases, the carpels may be united in the region of ovaries only, styles and stigmas remaining free, as in Fams. Caryophyllaceae (Fig. 110, B) Linaceae, Plumbaginaceae, Hypericaceae, etc., or in the regions of ovaries and styles only, the stigmas remaining free, as in Fam. Malvaceae (Fig. 110, A) ; or, in the regions of styles and stigmas, the ovaries only

* In fact, the so-called gynobasic type of style is nothing but the lateral one.

† Such a gynaecium is called **pseudomonomerous**. In the majority of families having syncarpous gynaecia the stigmas are axially developed on the midribs of the carpels and are termed **axillary**. In a few families, however, like Rosaceae, Dipsacaceae, etc., they are fused situated over the lines of fusion of the margins of the carpels, as these lines are popularly known as 'commisures', such stigmas are called **commisural**. In gynaecia known as **syngamous**, however, there is no union between the carpels to form the ovary, as such, there is neither the style nor the stigma.

remaining free, as in Fams. Apocynaceae (Fig. 110, C), Asclepiadaceae (Fig. 110, D), *etc.* The ovary of a monocarpellary gynaecium has a single **loculus** or **chamber**. In such an ovary, the united margins of the carpel is called the **ventral suture**, and the line along which the carpel is folded, corresponding to the midrib of the foliage leaf, is called the **dorsal suture**. The ovary of a syncarpous gynaecium, on the other hand, may be **unilocular** (1-chambered), as in papaw (*Carica papaya*) of Fam. Caricaceae, poppy (*Papaver somniferum*) of Fam. Papaveraceae, *etc.*, **bilocular** (2-chambered), as in Fams. Acanthaceae, Oleaceae, Scro-

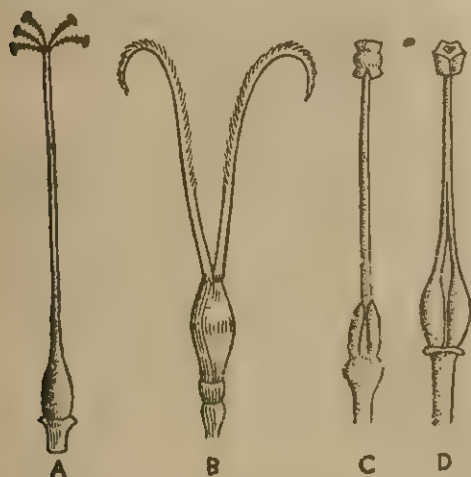


FIG. 110. TYPES OF UNION OF CARPELS

phulariaceae, *etc.*, **trilocular** (3-chambered), as in Fams. Euphorbiaceae, Liliaceae, Amaryllidaceae, *etc.*, and **plurilocular** or **multilocular** (many-chambered), as in Fams. Malvaceae, Sterculiaceae, Rutaceae, *etc.* It is to be noted that the number of loculi or chambers produced internally in a compound ovary by the *septa* or partition walls, usually correspond to the number

of carpels taking part in the formation of the ovary. But, when the union of carpels is complete, the *septa* are not present, and the ovary becomes unilocular, in which just the traces of its compound nature may be visible. This latter case is designated as **paracarpous** in distinction to the former one, which is really **syncarpous**. Both these types are collectively termed as **coenocarpous**. It has already been pointed out that, with reference to its position to other sets of floral members, the ovary may be **superior** or **inferior**. Within each ovary there are one or more **ovules** or **megasporangia**, the future seeds of the plant, which usually develop along one or more ridges of tissue (**placentae**) produced on the inner surface of the united margins

of carpel or carpels. In some cases, the placentae are restricted, either towards the base or towards the apex of the ovary. It should be noted that the position of the ovule within the ovary determines the position of the placenta.

CARPEL POLYMORPHISM

In the family Compositae and in some rare cases, as in a few species of *Chenopodium* and *Artiplex* of Fam. Chenopodiaceae, as well as in *Polygonum* (Fam. Polygonaceae), a difference in forms between the fruits is noted. Consequently, it is believed that there exists a difference between their carpels also. This phenomenon has been referred to as the **polymorphy of carpels** or **heterocarpy**. Saunders put forward a theory, named '*Theory of Carpel Polymorphism*', in which she recognised three distinctly different types of structure of the carpels. The first type or the **valve carpel** is regarded as a modified type of leafy organ, which is present in apocarpous pistils only. Such a carpel possesses only one style and one stigma. The second type or the **solid carpel**, which is supposed to be a reduced one, is found in the majority of the syncarpous pistils. In association with the solid carpels there may be valve carpels present also; in such cases (e.g., members of Fam. Cruciferae) the former are usually fertile, while the latter are sterile. The style of the carpel, if present, may be simple or bifid. The third type or the **semi-solid carpel** or **pseudo-valve** exhibits some of the characteristics of both the previous two types. If there is a style, it bears a bifid stigma at its tip. The typical examples of semi-solid carpels can be found in the families Papilionaceae, Berberidaceae and Orchidaceae.

This theory was adversely criticised firstly by Eames (1931), and at present it is completely discarded by the majority of workers.

PLACENTATION (FIG. 111)

The **placentation** is the mode of origin and arrangement of the placentae within the ovary, and it appears to be a somewhat constant and uniform character, which helps in the classification of plants. In the gymnosperms (among seed plants), the carpels do not unite and always remain open. Hence, there is neither any ovary nor any placenta, and the ovules are borne

directly on the carpels. In the angiosperms, on the other hand, there are a few distinct types of placentation noted.

Though botanists do not agree unanimously, yet it is usually considered that in primitive families with a simple ovary (e.g., Ranunculaceae, Magnoliaceae, Anonaceae, Leguminosae, etc.), the placenta is usually solitary, and is situated parietally on



FIG. 111. PLACENTATION

A, an open carpel ; B, marginal ; C, parietal ; D, axile ; E, free central ; F, central ; G, superficial ; H, basal.

the two united margins of the some carpel (ventral suture) bearing an ovule. This is termed as the **parietal** placentation. According to some botanists, this type of placentation is also referred to as the **marginal** or **ventral** placentation. This placental type may also be found in a compound ovary, where it occurs along two evolutionary lines. In one case, it might have come

from a gynaecium having a number of incurved carpels, which stood very closely to one another and ultimately fused by their margins. In such a case, a unilocular compound ovary results, in which each placental zone is produced from the united margins of two adjacent carpels. The second evolutionary line of development is supposed to have been a derivation from the axile type of placentation, discussed below. The central placental zones of an axile placentation separate out and recede towards the ovarian walls. Thus, the plurilocular condition of the ovary is changed into a unilocular one, though the numbers of carpels and placentae remain the same as before. Some workers designate this second type as **falsely parietal**, which is considered as more advanced than the parietal and axile placentations. Common examples of parietal placentation can be found in the families Cruciferae, Capparidaceae, Papaveraceae, Cucurbitaceae, Passifloraceae, some members of Gentianaceae and Orchidaceae.

A second type of placentation is known as **axile**. An axile placentation results by the union and fusion of the margins of incurved carpels at or near about the centre of a compound ovary. The ovules are borne on the axis formed by such unions. It should be noted, however, that there is no stem axis present in such a case. In a compound ovary having axile placentation, the number of placentae usually corresponds to the number of carpels involved, and generally a loculus represents a carpel. This is the most common type of placentation found among plants.

The third type of placentation found in a compound ovary is called the **free central** placentation. This type is generally believed to have been derived from the axile type of placentation. It is supposed that in this case, the central column as well as its placentae persist, but the septa break down and may finally disappear. Consequently, the compound ovary becomes unilocular. The free central type of placentation is found in families Caryophyllaceae, Primulaceae, Santalaceae, Lentibulariaceae, and in some genera like *Dionaea* of Fam. Droseraceae.

A further reduction of the central column found in the free central type of placentation gives rise to the fourth type, known as the **basal** placentation. Here, the central axis is reduced to a minute knob-like structure, from the tip of which a single

ovule appears. In extreme cases, the axis is completely lost, and the ovule seems to have arisen from the base of the loculus. Common examples of this type can be found in families Compositae, Amaranthaceae, Polygonaceae, etc.

The last or the fifth type of placentation is designated as the **lamellate** or **superficial** placentation. In this type, the placental zones are situated over one or more flat and broad lamellate areas within the compound ovary. These areas may be superficial or may appear as plate-like partition walls. Typical examples of lamellate placentation are found in the genera *Nymphaea* and *Nuphar* of Fam. Nymphaeaceae, *Papaver* of Fam. Papaveraceae, and *Alisma* and *Butomus* of Fam. Alismataceae.

THE OVULE

The **ovule** or **megasporangium** shows great uniformity of structure and contents in each species; it is converted into the **seed** after fertilization. A typical angiospermic ovule consists of a body made up of an oval mass of tissue, the **nucellus**, which is surrounded by one* or two coats, called the **integuments**. The integuments do not invest the nucellus completely, but leaves a small pore or **micropyle** at the top. The ovule is usually provided with a stalk, the **funiculus** or **funicle**, by means of which it remains attached to the placenta. The broader basal part of the ovule, where the nucellus and the integuments meet, is called the **chalaza**. Through the funiculus a vascular supply from the placenta reaches the chalazal region, where it distributes itself. When a portion of the funiculus is fused with the integuments, the fused part of the stalk is known as the **raphe**.

A longitudinal section of an ovule (Fig. 112) generally reveals the presence of a conspicuous and large oval body, called the **embryo sac** (representing the female gametophyte), embedded in the tissue of the nucellus, near and directly below the micropyle. Before fertilization, it typically contains eight nuclei. Of these, three collectively constitute the **egg apparatus**, and occupy the

* In some plants, such as *Loranthus longiflorus* (Fam. Loranthaceae), *Santalum album* (Fam. Santalaceae), *Balanophora dioica* (Fam. Balanophoraceae), etc., the integuments are entirely absent.

micropylar end of the embryo sac ; it consists of a central cell, the egg or **oosphere** or **ovum**, and two **synergids** or helping cells, one on each side of it. At the opposite or chalazal end there is another group of three nuclei, which collectively form the **antipodal cells** or **antipodals**. At the centre there is found a

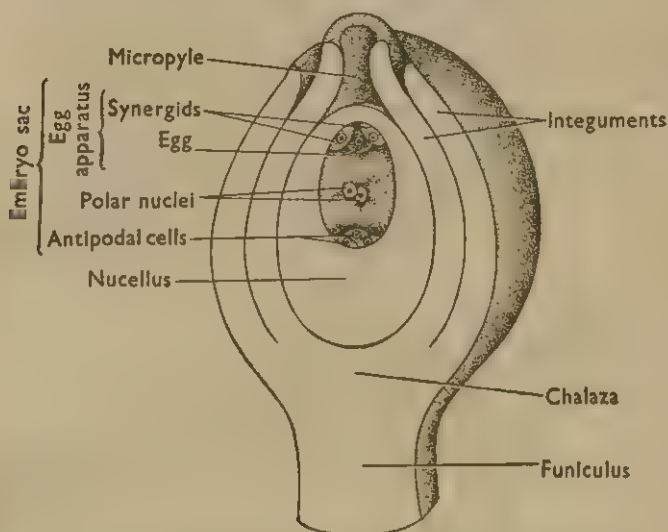


FIG. 112. LONGITUDINAL SECTION THROUGH AN OVULE

pair of nuclei, called the **polar nuclei**, which may subsequently fuse together to form a **definitive nucleus** or **secondary nucleus** or **polar fusion nucleus**. In a fully formed ovule, the three micropylar nuclei along with the surrounding cytoplasm become enclosed within delicate walls ; the antipodal nuclei are also usually separated by thin cellulose walls, but the two polar nuclei remain naked.

DEVELOPMENT OF THE EMBRYO SAC OR FEMALE GAMETOPHYTE (Figs. 113 & 114)

An ovule may be designated as **crassinucellate** (Fig. 113, B) or as **teninucellate** (Fig. 113, A). In the former case, the megaspore mother-cells are deeply embedded in a massive nucellus, while in the latter, the nucellus is rather small and

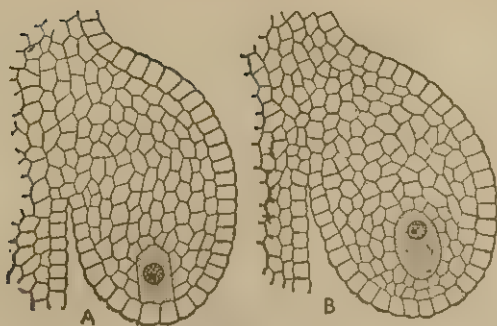


FIG. 113. L. S. THROUGH DEVELOPING OVULES
A, Tenuinucellate type ; B, Crassinucellate types.

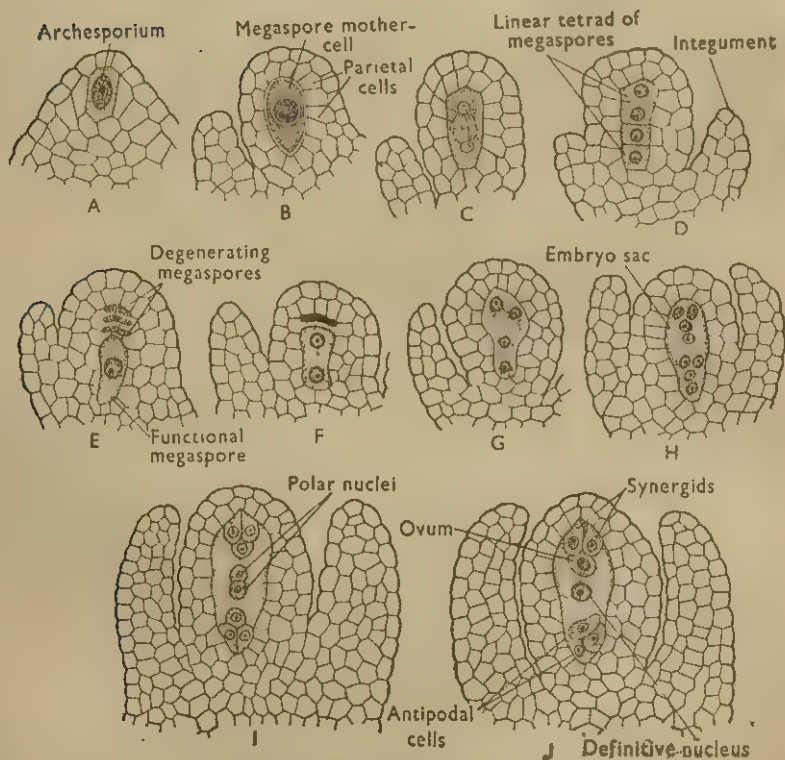


FIG. 114. STAGES IN THE DEVELOPMENT OF THE EMBRYO SAC
OR FEMALE GAMETOPHYTE.

delicate, and usually a solitary megaspore mother-cell lies just below the epidermis.

Early during the development of an ovule, one or a few hypodermal cells at the apex of the primordium stand out conspicuously on account of their larger size, denser cytoplasm and larger nuclei ; these cells constitute the **archesporium**. In crassinucellate ovules, the cells of the archesporium divide, mainly periclinally, and give rise to the inner **sporogenous cells**, and the outer **primary parietal cells**, one or more of these sporogenous cells function as **megaspore mother-cells**. In tenuinucellate ovules, on the other hand, the archesporium usually consists of the single terminal cell of an axial row of cells. This solitary cell, generally, becomes the sporogenous one later on, and behaves as the megaspore mother-cell.

The megaspore mother-cell undergoes meiotic divisions, and generally gives rise to a **linear tetrad of megaspores**, though occasionally other types of grouping are also met with. In a typical tetrad, the chalazal member usually survives, the other three undergoing degeneration. The nucleus of this surviving megaspore then divides mitotically, and the two daughter nuclei travel towards the two poles (of the germinating megaspore). These two nuclei, in their turn, divide twice mitotically to give rise to eight nuclei altogether. This is the eight-nucleate condition of the normal type of embryo sac. The subsequent stages in the disposition of these nuclei have already been considered before.

Types of ovule (Fig. 115)

Usually there are five common types of ovule, as discussed below :•

Orthotropous or **atropous** or straight, when the ovule is erect, so that the micropyle, chalaza, and funiculus lie on a straight line. In this case, the micropyle lies at the apex, and the chalaza at the base of the ovule, as in black pepper (*Piper nigrum*), long pepper (*Piper longum*) and other plants of Fam. Piperaceae, *Polygonum orientale*, dock (*Rumex vesicarius*) and other plants of Fam. Polygonaceae, members of Fams. Nyctaginaceae, Urticaceae, Cistaceae, etc.

Anatropous or inverted, when during the early stages of development the ovule bends over in such a way, that the micropyle comes to lie along the side of the funiculus. In this case, the micropyle is directed towards the base, and a part of the funi-

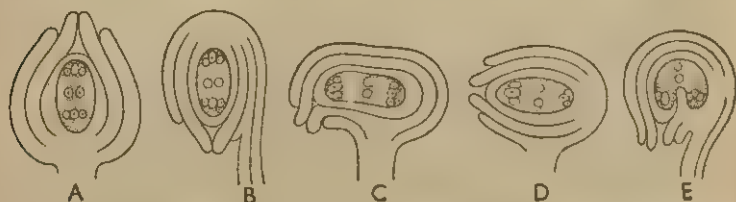


FIG. 115. TYPES OF OVULE (in median longitudinal section)

A, orthotropous ; B, anatropous ; C, campylotropous ; D, hemianatropous ; E, amphitropous.

culus is fused with the body of the ovule forming the **raphe**. It is the most common type of ovule and can be found in a large number of families belonging to dicotyledons as well as monocotyledons.

Campylotropous, when the ovule is somewhat curved, as is found in some members of the families Resedaceae, Leguminosae, etc.

Amphitropous, when the ovule is highly curved, as a result of which, the embryo sac even is bent in the form of a horseshoe, as is found in the families Alismataceae, Butomaceae, as well as in the order Centrospermae.

Hemianatropous or **hemitropous**, when the ovule is so bent that its long axis lies more or less at right angles to the funiculus, as can be found in *Ranunculus* sp. (Fam. Ranunculaceae), and a few members of Fam. Liliaceae.

Besides these, there are also a few other types, which are sometimes met with in different families.

Positions of ovule (Fig. 116)

As to the position and direction inside the ovary, the ovules may be **horizontal**, when these grow horizontally from one side of the ovarian wall, i.e., when these are neither turned upwards nor downwards, as in *Podophyllum emodi* (Fam. Berberidaceae); **ascending**, when these arise obliquely upwards, usually from

the side of the ovarian wall and not from the base, as in some *Ranunculaceae* ; **erect**, when these arise from the base of the ovary in an upright manner, as in Fam. *Compositae* ; **pendulous**, when these hang downwards from the side or from the top of the ovarian wall, as in the flax (*Linum usitatissimum*) of Fam.

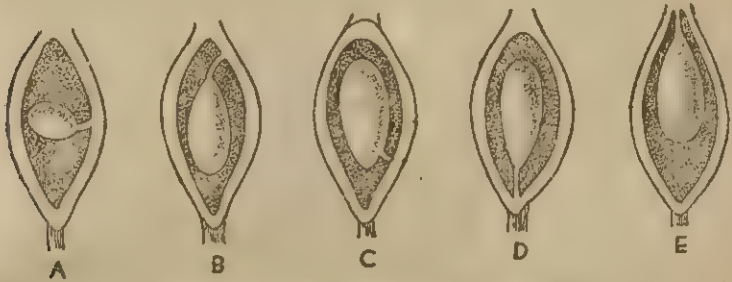


FIG. 116. POSITIONS OF OVULE (in median longitudinal section of the ovary) A, horizontal ; B, pendulous ; C, ascending ; D, erect ; E, suspended.

Linaceae, castor (*Ricinus communis*) of Fam. *Euphorbiaceae*, *etc.* ; or **suspended**, when these hang perpendicularly downwards from the very top of the ovarian chamber, as in custard apple (*Anona squamosa*) and other plants of Fam. *Anonace*, Rangoon creeper (*Quisqualis malabaricum*) of Fam. *Combretaceae*, *etc.*

A TYPICAL OR MODEL FLOWER

A typical flower has the following characters: the four whorls of floral leaves—calyx, corolla, androecium and gynaecium—must be present: there should be one series of each whorl ; the number of floral leaves in each and every whorl should be the same ; the successive whorls should alternate ; the floral leaves in each whorl should be of the same shape, size, colour, *etc.*, and should be free from one another as well as from the members of the neighbouring whorls.

A typical flower can rarely be found. However, the flower of *Bryophyllum calycinum* (Fam. *Crassulaceae*) approaches a typical flower, except in the fact that the sepals are more or less united.

Modes of deviation from the typical form

One or more of the four whorls may be absent, and thus the flower becomes an **incomplete** one.

Chorisis. One or more whorls may be branched, as in mustard (*Brassica nigra*) of Fam. Cruciferae, or doubled, so that instead of one series of each whorl there are two or more series.

The members of one or more whorls may increase (**pleiomery**) or decrease in number (**oligomery**).

The members of a whorl, instead of being alternate, may be opposite to the members of another whorl. Thus, in Fams. Rhamnaceae, Portulacaceae, Vitaceae, Geraniaceae, etc., the outer whorls of stamens are opposite to the petals instead of alternating with them.

The floral leaves of a whorl may not be alike in size and form, and thus, the flower becomes an irregular one. Thus, corona, labellum, etc., increase the irregularity of flowers.

The floral leaves of a whorl may be united instead of being separate. Thus, the flowers with cohesion or adhesion in floral parts are not typical.

FLORAL DIAGRAMS AND FORMULAE

FLORAL DIAGRAM (Figs. 117 & 118). The floral diagram is the ground plan of a flower showing the *relative arrangement of floral members in relation to the mother axis*. In order to get an idea of a floral diagram, a flower bud should be cut across, and then carefully examined from above with the aid of a hand lens. It will be found that the floral leaves form successive circles or spirals. The stamens are usually represented by small two- or four-lobed structures. The number and position of the carpels are indicated within the innermost circle. The cohesion or adhesion in the whorls are indicated by small connecting lines. The mother axis is indicated by a solid dot at the top of the diagram. The side of the flower nearest to the axis is called the **posterior side**, while the other, away from the axis, the **anterior side**.

In a regular, actinomorphic flower (Fig. 117, A & B) the vertical plane passing through the centre of the diagram and the mother axis is known as the **median plane**, which divides the flower into two equal and similar halves, right and left. The vertical plane passing through the centre, and cutting the median plane at right angles is known as the **lateral plane**, which divides the flower into two equal halves, the posterior, and the anterior.

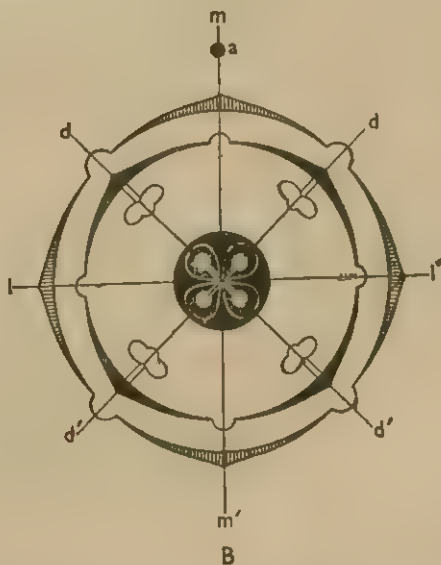
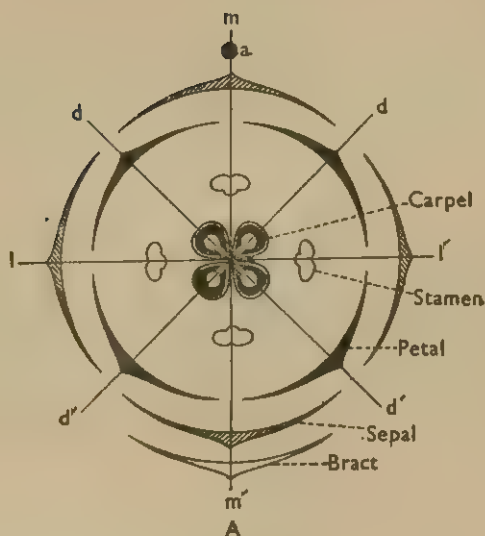


FIG. 117. FLORAL DIAGRAMS

A, of a bracteate flower, having the members of each whorl free ; B, of an ebracteate flower, showing cohesion and adhesion of floral parts ; a, mother axis ; mm', median plane ; ll', lateral plane ; dd', diagonal plane.

The two vertical planes, which bisect the angles formed by the median and lateral planes, are known as the **diagonal planes**, each of which divides the flower into two equal and similar halves. The floral diagrams of a few common flowers are shown in Fig. 118.



FIG. 118. FLORAL DIAGRAMS

A, of mustard ; B, of pea ; C, of water lily ; D, of potato ; E, of madar ; F, of tuberose ; G, of the staminate flower of gourd ; H, of the pistillate flower of gourd.

FLORAL FORMULA. The different whorls of a flower, their number, cohesion, and adhesion can be represented by a formula known as the *floral formula*. Certain symbols are used in this connection. Thus, K stands for calyx, C for corolla, P for perianth, A for androecium, G for gynaecium, G for superior ovary, G for inferior ovary, ()

for cohesion of parts, [] or \frown for adhesion of parts, α for numerous members in a whorl, σ or φ for a hermaphrodite flower, σ for a male flower, φ for a female flower, \oplus for an actinomorphic flower, and \downarrow or $\cdot\downarrow$ for a zygomorphic flower. The number following each symbol indicates the number of parts in that particular whorl. Cohesion is indicated by enclosing the number within brackets, and adhesion by a straight or curved line drawn above from one letter to the other or by a box bracket enclosing the two letters. If the ovary be inferior, a bar is drawn above the letter G, and if it be superior, the bar is placed below. The α sign denotes that the members of the whorl are numerous.

The floral formulae of a few common flowers are given below :

(i) Flower of mustard (*Brassica nigra*) of Fam. Cruciferae is represented by the formula $\sigma \oplus K_{2+2} C_{\times 4} A_{2+4} \underline{G}_{(2)}$.

K_{2+2} indicates that the calyx consists of four free sepals, which are arranged in two whorls of two each. $C_{\times 4}$ indicates that the corolla consists of four free petals arranged crosswise. A_{2+4} indicates that the androecium consists of six stamens in two whorls, the outer one of which contains two stamens, while the inner one of four stamens. $\underline{G}_{(2)}$ indicates that the gynaecium consists of two united carpels with a superior ovary.

(ii) The flower of brinjal (*Solanum melongena*) of Fam. Solanaceae is represented by the formula $\sigma \downarrow K_{(5)} \overline{C}_{(5)} A_5 \underline{G}_{(2)}$.

$K_{(5)}$ indicates that the calyx consists of five united sepals. $\overline{C}_{(5)}$ indicates that the corolla consists of five united petals. A_5 indicates that the androecium consists of five stamens and the line on the top denotes that the stamens are epipetalous. $\underline{G}_{(2)}$ indicates that the gynaecium consists of two united carpels with a superior ovary.

(iii) The flower of gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae is represented by the formulae $\sigma K_{(5)} C_{(5)} A_{(2)+(2)+1}$ and $\varphi K_{(5)} C_{(5)} \overline{G}_{(3)}$.*

* Some prefer to put these as $\sigma K_{(5)} C_{(5)} A_{(3)} G_0$ and $\varphi K_{(5)} G_{(5)} A_0 \overline{G}_{(3)}$.

$K_{(5)}$ indicates that the calyx consists of five united sepals. $C_{(5)}$ indicates that the corolla consists of five united petals. $A_{(2)+(2)+1}$ indicates that in the male flower, the androecium consists of five stamens in three bundles. $\overline{G}_{(3)}$ indicates that the gynaecium consists of three united carpels with an inferior ovary.

(iv) The flower of *Calotropis procera* (Fam. Asclepiadaceae) is represented by the formula $\sigma^{\circ} \oplus K_{(5)} C_{(5)} [A_5 \overline{G}_{(2)}]$.

$K_{(5)}$ indicates that the calyx consists of five united sepals. $C_{(5)}$ indicates that the corolla consists of five united petals. A_5 indicates that the androecium consists five stamens, and the box bracket denotes that these are united with the carpels. $\overline{G}_{(2)}$ indicates that the gynaecium consists of two united carpels with a superior ovary.

(v) The flower of tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae is represented by the formula $\sigma^{\circ} \oplus \overbrace{P_{(3+3)} A_{3+3}} \overline{G}_{(3)}$.

$P_{(3+3)}$ indicates that the perianth consists of six united perianth leaves in two whorls. A_{3+3} indicates that the androecium consists of six stamens in two whorls, and the line above denotes that these are united with the perianth leaves. $\overline{G}_{(3)}$ indicates that the gynaecium consists of three united carpels with an inferior ovary.

ECONOMIC IMPORTANCE OF FLOWERS

In most cases, flowers have got only an aesthetic value, and as such, are cultivated purely for ornamental, festive and decorative purposes. The Hindus use them extensively in their worships. Flowers like rose, jasmine, lavender, orange, carnation, etc., yield very valuable perfumes, which are obtained by the distillation of the fragrant oils present in the blossoms. The flowers of hops (*Humulus lupulus*) of Fam. Moraceae and of *Bassia latifolia* (Fam. Zapotaceae) are cultivated for the manufacture of beverages. Flowers, such as lotus, orange, etc., are important sources of honey, which is derived from their nectar-secretions and kept in store by bees. The edible parts of some vegetable crops like cauliflower and broccoli (both belonging to Fam. Cruciferae) are nothing but huge clusters of abortive buds. The flowers of *Sesbania*, gourd, horse radish, etc., are usually fried and taken as food. The

dried unopened flower buds of clove (*Eugenia caryophyllata*) of Fam. Myrtaceae form the source of 'clove oil' and have great commercial importance. The flowers of *Fuchsia* (Fam. Onagraceae) yield 'fuchsine', a red colouring matter, much used as a staining reagent.

CHAPTER VI

THE INFLORESCENCE

The flowers may arise singly in the axils of the leaves, as in China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae, or the main axis may terminate in a flower. In some cases, the flower buds may also be borne on special branches or branch systems. The special branch or branch system bearing a solitary flower or a cluster of flowers is called **inflorescence** or **anthotaxy**. Generally an inflorescence is *terminal*, because its branches develop at the top of the shoot. Very few are, however, *intercalary*, that is, the vegetative growth of the shoot continues beyond such inflorescences. In some other cases (e.g., *Drimys* of Fam. Magnoliaceae), the terminal bud of the shoot becomes abortive, and a cluster of axillary inflorescences, which is really intercalary in nature, appears near about the apex of the shoot giving rise to a *pseudo-terminal* inflorescence. Sometimes, the terminal inflorescences are extremely reduced and are developed in a highly condensed manner on suppressed side-shoots. As a consequence, the inflorescences seem to appear directly from the surface of the main trunk (**trunciflory**) or its branches (**remiflory**). Such a condition is generally referred to as **cauliflory** or **cladanthly**. Examples of cauliflory can be found mainly in the tropical trees, like cocoa (*Theobroma cacao*) of Fam. Sterculiaceae, cannon-ball tree (*Couroupita guianensis*) of Fam. Lecythidaceae, jack-fruit (*Artocarpus integra* = *A. integrifolia*) of Fam. Moraceae and others. Sometimes epiphyllous inflorescences develop from the surface of the lamina, as in *Helwingia japonica* (Fam. Araliaceae), *Begonia prolifera* and *B. sinuata* (Fam. Begoniaceae), *Duloniga acuminata*, etc.

The study of inflorescence has got a profound taxonomic significance. In a number of families the inflorescence is characteristically constant and thus helps in their identification, as in the families Cornaceae, Umbelliferae, Compositae, Labiatae, Amaryllidaceae, Gramineae, etc. In some cases, it is helpful in determining tribes or genera, as in *Hamelia* (Fam. Rubiaceae),

Heliotropium (Fam. Boraginaceae), *Smilax* (Fam. Liliaceae), *Borassus* (Fam. Palmae), etc.

The stalk of a solitary inflorescence (Fig. 119, A) or the main axis of an inflorescence bearing flowers (Fig- 119, C) is called the **peduncle**.* If this axis branches and each branch bears a flower, the main axis is even now called a peduncle, and the stalk of each flower, a **pedicel** (Fig. 119, C). Flowers with pedicels are called **pedicellate** flowers, and those



FIG. 119. THE DIFFERENT KINDS OF FLOWER- AND INFLORESCENCE-BEARING REGIONS

A, Peduncle of china rose ; B, Scape of onion ; C, Peduncle and pedicel of mustard ; D, Receptacle of sunflower.

without them, **sessile**. An elongated and simple or branched peduncle is also called a **rachis**. When the peduncle is more or less dilated and flattened, it is called the **receptacle** (Fig. 119, D). The receptacle may be conical, concave, convex, pear-shaped or cup-like. The extremity of the peduncle or pedicel bearing the floral parts is often called the **thalamus** instead of receptacle. If the peduncle remains simple, *i.e.*, unbranched,

* The unbranched and leafless peduncle in onion (*Allium cepa* Fig. 119, B) of Fam. Liliaceae, tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae, etc., is known as the **scape**.

the inflorescence is *simple*, if branched, it is *compound*. Flowers developing in the axils of bracts are called **bracteate** flowers and if otherwise, **ebracteate**. In acaulescent plants, the flowers are borne on a special unbranched axis, known as the **scape** or **radical peduncle**.

Types of inflorescence

There are four types of inflorescence : racemose (indefinite or indeterminate), cymose (definite or determinate), mixed, and special.

I. RACEMOSE INFLORESCENCE

A **racemose** or **indefinite** inflorescence is one, in which the rachis, whether simple or branched, never ends in a flower, but it continues to elongate by means of a persistent growing point. It produces stalked or sessile lateral flowers, either directly or on its branches in more or less indefinite succession. The order of opening of the flowers is **acropetal** or ascending, because the oldest flower is near the base of the inflorescence and the youngest one near the growing point. Moreover, when either due to unequal development of the pedicels, or by the partial or total suppression of the successive internodes of the axis, all the flowers are brought to the same level, it is found that the youngest flower is situated near the centre (*i.e.*, the free-growing point of the axis) and the oldest outside, so that the order of opening of the flowers is from outside inwards, *i.e.*, **centripetal**. In all cases, however, it is evident that the flowers are produced in the axils of bracts, developed at each node of the axis, and the secondary branches grow less vigorously than the axis.

Several types of racemose inflorescence are recognized and these are described below.

SIMPLE RACEMOSE INFLORESCENCE

Stalked or sessile flowers are directly borne on the main axis.

Flowers pedicellate

Raceme (Fig. 120, A & B). The main axis is elongated and more or less equally pedicellate flowers are directly borne on it. The common examples are *Polanisia icosandra* (= *Cleome viscosa*) and *Gynandropsis gynandra* (= *G. pentaphylla*) of Fam. Cappari-



FIG. 120. RACEMOSE INFLORESCENCE
A-B, raceme ; C-D, panicle ; E-F, corymb.

daceae, radish (*Raphanus sativus*) and mustard* (*Brassica nigra*) of Fam. Cruciferae, *Crotalaria juncea* of S.F. Papilionaceae (Fam. Leguminosae), *Asparagus recemosus* (Fam. Liliaceae), etc.

Corymb (Fig. 120, E & F). Similar to raceme, but it differs from the former in having a relatively shorter main axis, and the flowers, due to unequal development of their pedicels, are nearly brought to the same level. The familiar examples are candytuft

* In young condition, the inflorescence of mustard is a corymb, but later on, it become a raceme.

(*Iberis odorata*) of Fam. Cruciferae, *Cassia auriculata* of S.F. Caesalpiniaceae (Fam. Leguminosae), etc.

Umbel (Fig. 121, A & B). The rachis is entirely suppressed in this case. The flowers are borne on pedicels of more or less equal length, and these apparently appear to arise from a common point on the suppressed rachis, resembling an open umbrella. The bracts collectively form an involucre at the base of these pedicellate flowers. The familiar

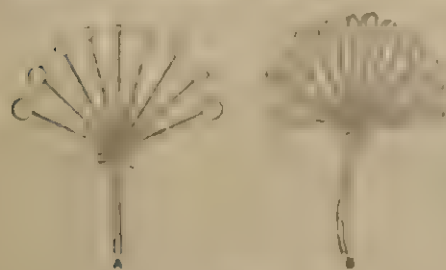


FIG. 121. SIMPLE UMBEL

example is Indian pennywort (*Hydrocotyle asiatica*) of Fam. Umbelliferae.

Flowers sessile

Spike (Fig. 122, A & B). Just like the raceme, the axis is elongated, but the flowers are nearly or completely sessile. The common examples are prickly chaff flower (*Chorizanthe aspera*) and *Desmodium canadense* of Fam. A. to this case *Adiantum caudex* (Fam. Acanthaceae), etc.



FIG. 122. SIMPLE AND COMPOUND SPIKES

A, B, simple spike; C, D, compound spike

There are several modifications of spike as follows:

Spadix (Fig. 123, A-C). This is a modification of spike, in which the main axis is thick and fleshy and bearing unisexual and chactate flowers, as is well seen in the common arum (*Colocasia antiphotum*) and many plants of Fam. Araceae. In these cases, the whole inflorescence is enclosed and protected by a large spathe. In some aroids, as in *Acorus calamus*, this spathe

may be absent. The pistillate flowers are always found towards the base of axis the staminate ones toward the tip where the sterile ones are situated in between these two. The extreme terminal portion is barren, and is known as the *appendix*.

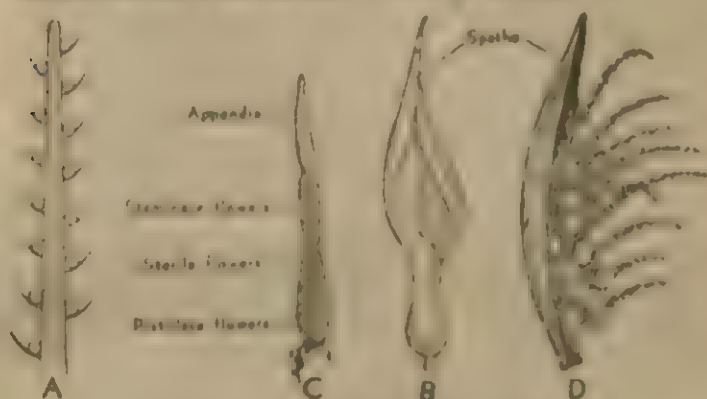
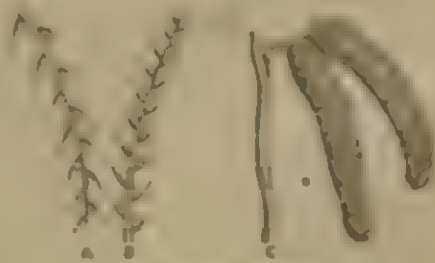


FIG. 123. SIMPLE AND COMPOUND SPADIX
A-C, simple spadix; D, compound spadix

The inflorescence of banana (*Musa sapientum*) is a very important one. It is a very large and branched inflorescence, the main axis is very thick and woody, and the flowers are very large. The inflorescence is a very important part of the banana plant, and it is very large and branched. The inflorescence is a very important part of the banana plant, and it is very large and branched. The inflorescence is a very important part of the banana plant, and it is very large and branched.

Catkin (Fig. 124). The inflorescence of the catkin is a very important one. It is a very large and branched inflorescence, the main axis is very thick and woody, and the flowers are very large. The inflorescence is a very important part of the catkin plant, and it is very large and branched. The inflorescence is a very important part of the catkin plant, and it is very large and branched. The inflorescence is a very important part of the catkin plant, and it is very large and branched.



Fam. Moraceae, *Trewia nudiflora* and *Acalypha hispida* of Fam. Euphorbiaceae, *Salix tetrasperma* (Fam. Salicaceae), etc.

Spikelet (Fig. 125). It is the inflorescence of grasses (Fam. Gramineae) and the sedges (Fam. Cyperaceae). Usually each spikelet bears several flowers (but one-flowered in paddy). In the *Panicum*-type of grass flower, the whole inflorescence bears at its base two sterile bracts, called **empty glumes**. Above these, there are one or more fertile glumes, called **flowering glumes** or **lemmas**, each of which bears in its axil a sessile flower. Above each flowering glume there comes a two-nerved bracteole, the

palea. The spikelets may be either sessile in an elongated axis, as in wheat (*Triticum aestivum* = *T. vulgare*), or they are produced on a more or less branched axis, as in the oat (*Avena sativa*).

Capitulum or head (Fig. 126). In this type of racemose inflorescence, the main axis is much shortened and broadened out to form a flat or a more or less convex receptacle, on which a number of small, sessile flowers, called **florets**, are arranged in such a manner that the outer

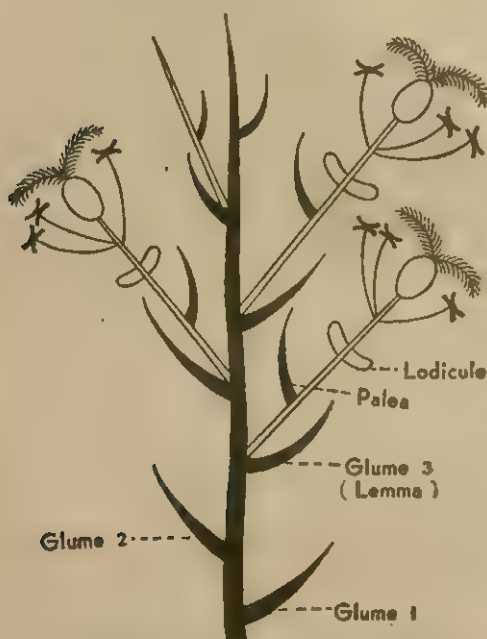


FIG. 125. SPIKELET OF A GRASS
(Diagrammatic).

florets are older than the inner ones, so that, the order of opening of the florets is outside inwards, i.e., **centripetal**. The base of the receptacle is surrounded by conspicuous bracts forming an involucre. The florets are often distinguished into two kinds* :

* It should be noted that in some cases, as in *Blumea* sp., *Vernonia* sp., *Chrysanthemum* sp., and some varieties of marigold (*Tagetes patula*), there is no differentiation between the disc and the ray florets.

those at the periphery with strap-shaped corolla are called **ray florets**, which are more conspicuous than the central ones, known as **disc florets**, which have tubular corolla. The florets, when arise in the axils of rudimentary scaly bracts (paleae), are called **paleated** ; when the florets are without any palea, they are



FIG. 126. CAPITULUM

A-B, capitulum ; C, vertical section of the same ; D, disc floret ; E, ray floret.

said to be **non-paleated**. The sunflower (*Helianthus annuus*), *Dahlia* sp., *Cosmos* sp., *Tridax procumbens* and the majority of plants belonging to Fam. Compositae have this characteristic type of inflorescence.

COMPOUND RACEMOSE INFLORESCENCE

Stalked or sessile flowers are borne on the branches of the main axis.

Compound raceme or panicle (Fig. 120, C & D). In this type of inflorescence, each branch of the main axis produces a cluster of stalked flowers like raceme. Examples are found in mango (*Mangifera indica*) of Fam. Anacardiaceae, margosa (*Melia azadirachta*) and mahagony (*Swietenia mahagoni*) of Fam. Meliaceae, etc.

Compound corymb. When the branches of the main axis bear corymbs, a compound corymb is formed, as in *Spiraea corymbosa* (Fam. Rosaceae).

Compound spike (Fig. 122, C & D). When the branches of the main axis bear spikes, a compound spike is formed, as in oat (*Avena sativa*) of Fam. Gramineae, foxtail (*Amaranthus spinosus*) and *A. viridis* of Fam. Amaranthaceae, etc.

Compound umbel. This is essentially an umbel, which consists of small umbels in places of single flowers. The smaller bracts at the base of each secondary umbel constitute an *involucre*. The common examples are coriander (*Coriandrum sativum*), anise (*Foeniculum vulgare*) and some other plants of Fam. Umbelliferae.

Compound spadix (Fig. 123, D). In this case, the fleshy axis is repeatedly branched and usually bears unisexual flowers. When young, the whole inflorescence is enclosed in a large spathe or each branch is separately enclosed in smaller spathes. The common examples are coconut (*Cocos nucifera*), date palm (*Phoenix sylvestris*), betel nut (*Areca catechu*) and many other plants of Fam. Palmae.

Compound capitulum. In this case, each capitulum is comprised of a number of small capitula, surrounded by an involucre of bracts, as in *Echinops echinatus* (Fam. Compositae).

II. CYMOSE INFLORESCENCE

In the **cymose** or **definite inflorescence** the main axis does not elongate indefinitely, as in the racemose type, but is always terminated by a flower bud at an early stage. Subsequent flowers are produced directly lower down the main axis or on its branches, and these axes in their turn end in flower buds. When the main axis is elongated, the oldest flower is situated at the top and the youngest one at the base. Hence, the order of opening of flowers is from top downwards, *i.e.*, **basipetal**. On the other hand, when the main axis is shortened and expanded, the oldest flower is seen to occupy the central position while the youngest one is peripheral, so that the order of opening of flowers is from inside outwards, *i.e.*, **centrifugal**.



FIG. 127. SOLITARY FLOWER
OF CHINA ROSE.

There are several types of cymose inflorescence, and these are described below.

Solitary. It is the simplest of all types of cymose inflorescence. The axis remains unbranched and always terminates in a flower. The flowers of the common China rose (*Hibiscus rosa-sinensis*) of Fam. Malvaceae (Fig. 127), *Magnolia grandiflora* and *Michelia champaca* of Fam. Magnoliaceae, *Nymphaea lotus* and *Nelumbo nucifera* (= *Nelumbium speciosum*) of Fam. Nymphaeaceae, etc., are examples of this type.

Uniparous or monochasial cyme or monochasium. In this type, the primary axis ends in a flower after giving rise to only one

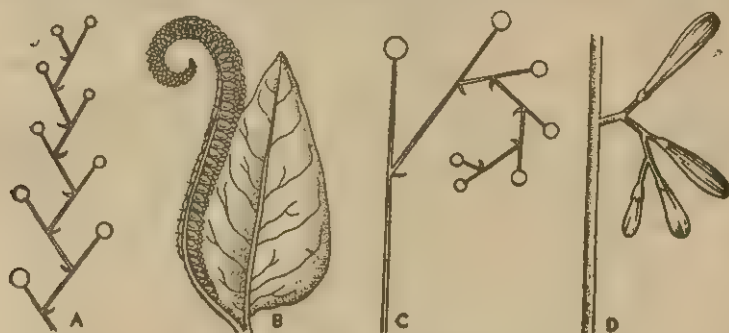


FIG. 128. MONOCHASIUM
A-B, scorpioid cyme; C-D, helicoid cyme.

daughter axis, which, in its turn, behaves in a similar manner. It is of two types as follows :

Scorpioid cyme or cincinnus (Fig. 128, A & B)—when the flowers are produced alternately on either side of the successive daughter axes, as in *Myosotis palustris*, *Symphytum* sp. and *Heliotropium ovalifolium* (all of Fam. Boraginaceae)*, some members of the families Hydrophyllaceae and Polemoniaceae. When the successively-formed lateral flowers lie in the same plane, a more or less fan-shaped inflorescence, called the **rhpidium** is formed.

Helicoid cyme or bostryx—when the flowers are produced on the same side (either clockwise or anti-clockwise) of the successive daughter axes, as in *Hamelia patens* (Fam. Rubiaceae, Fig. 128, C & D), day lily (*Hemerocallis fulva*) of Fam. Liliaceae, etc. When the successively-formed lateral flowers lie in the same plane, the inflorescence is termed as the **drepanium**.

* *Heliotropium indicum* bears flowers in double scorpioid cymes, also known as boragoid cymes.

If the axis gets straightened, the inflorescence is often confused with a raceme, from which it is distinguished in having bracts on the opposite side of the sympodial axis, as in tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae.

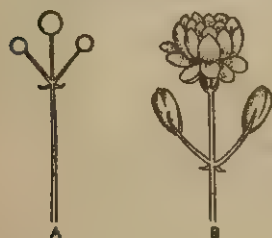


FIG. 129. DICHASIUM

Biparous or dichasial cyme or dichasium. In this case, the primary axis ends in a flower after giving rise to two daughter axes, which, in their turn, behave in a similar manner. Typical examples are *Clerodendrum* (= *Clerodendron*) *infor-*

tunatum (Fam. Verbenaceae), jasmine (*Jasminum* sp., Fig. 129) and *Nyctanthes arbor-tristis** of Fam. Oleaceae, pink (*Dianthus chinensis*) and many plants of Fam. Caryophyllaceae, etc.

Multiparous or polychasial cyme or polychasium or pleiochasium. In this case, the primary axis ends in a flower after producing more than two daughter axes in a whorled manner. The daughter axes also, in their turn, behave in a similar manner. *Calotropis procera* (Fam. Asclepiadaceae), *Dombeya mastersii* and *Kleinhovia hospita* of Fam. Sterculiaceae, etc., afford typical examples. It is often confused with the racemose umbellate inflorescence, from which it is distinguished in having the oldest flower at the centre.

III. MIXED INFLORESCENCE

Besides the aforesaid typical racemose and cymose inflorescences, several mixed types are frequently found. Thus, there may be combinations of two racemose types, such as raceme with spike, raceme with umbel, etc., or of a racemose type and a cymose one. It is found that the inflorescence of sunflower (*Helianthus annuus*) of Fam. Compositae, with respect to a single inflorescence, is racemose; but with respect to the main axis of the plant, the terminal inflorescence is the largest and opens first showing the cymose character.

The mixed inflorescence may be as follows :

Spicate cyme. When a spike is mixed with a cyme. In case of basil (*Ocimum sanctum*) of Fam. Labiatae, the inflorescence

*Placed under Fam. Verbenaceae by Shaw (1952).

with respect to a single cluster is cymose, while all the clusters taken together constitute a racemose type.

Cymose corymb or corymbose cyme. When the clusters of flowers look like a corymb, but have the oldest flower at the centre. The common examples are *Oldenlandia corymbosa*, *Ixora parviflora*, *I. coccinea* and many other plants of Fam. Rubiaceae, *Alstonia scholaris*, *Holarrhena antidysenterica* and many other plants of Fam. Apocynaceae, etc.

Fascicle. It is a modification of corymbose cyme. In this type, the successive axes are much shortened and so developed as to produce the flowers at the same level forming a flat-topped cyme, which resembles a corymb. Familiar example is sweet William (*Dianthus barbatus*, Fig. 130) of Fam. Caryophyllaceae.

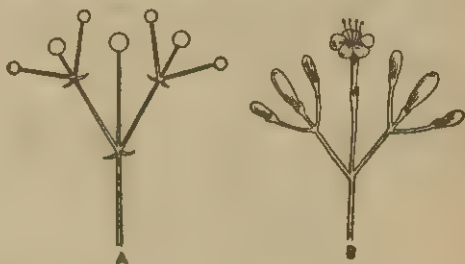


FIG. 130. FASCICLE

Thyrus. It is a condensed mixed type of panicle, in which the entire inflorescence is of the racemose type, but the later flowers are developed in the cymose fashion, as in *Syringa* of Fam. Oleaceae. When a thyrus is highly condensed, as in *Dipsacus* of Fam. Dipsacaceae, it is frequently confused with a capitulum. A closer examination, however, reveals that each flower has a separate whorl of bracts, and the manner of opening of flowers is centrifugal in both the directions.



FIG. 131. CYMOSE UMBEL

Cymose umbel or umbellate cyme. In this case, the clusters of flowers look like an umbel, but have the oldest flower at the centre, as in *Crinum asiaticum* (Fam. Amaryllidaceae), *Calotropis procera* (Fam. Asclepiad-

aceae), *Lantana camara*, *Lippia geminata* and *L. nodiflora* of

Fam. Verbenaceae, *Oldenlandia umbellata* (Fam. Rubiaceae),
Butomopsis lanceolata (Fam. Alismataceae, Fig. 131), etc.

IV. SPECIAL INFLORESCENCE

The following are the special forms of inflorescence :

Hypanthodium. This is a special type of inflorescence, in which the tip of the rachis is not only compressed and widened out, but also becomes fleshy and more or less hollow like a cup, leaving a minute opening at the apex, which is guarded by scales. Numerous small unisexual flowers are borne on its inner surface, the female flowers being towards the bottom and

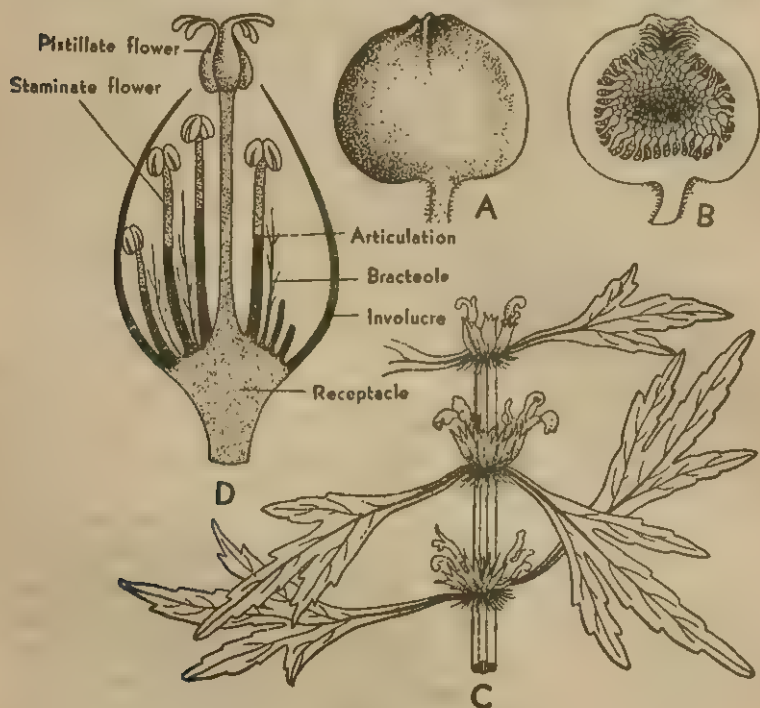


FIG. 132. SPECIAL FORMS OF INFLORESCENCE
 A-B, hypanthodium ; C, verticillaster ; D, cyathium.

the male ones towards the opening. The involucre of bracts are absent, but the rachis is subtended by one or two bracteoles.

Familiar examples are the fig (*Ficus cunia*, Fig. 132, A & B), banyan (*Ficus benghalensis*), and sacred banyan (*F. religiosa*) of Fam. Moraceae.

Verticillaster. This is a much condensed cymose inflorescence, each occurring in the axils of opposite leaves, bearing sessile or slightly stalked flowers. The whole inflorescence appears very much like a cluster of sessile flowers forming a verticel or false whorl at the node. During development, the primary axis often gives rise to a true biparous cyme, and the succeeding daughter axes to scorpioid cymes. The common examples are *Leonurus sibiricus* (Fig. 132, C), *Leucas aspera* and the majority of plants of Fam. Labiatae.

Cyathium. It is a special type of cymose inflorescence, which looks like a single flower, and is found in *Poinsettia pulcherrima* (Fig. 132, D), *Pedilanthus tithymaloides* and *Euphorbia hypericifolia* of Fam. Euphorbiaceae. Here the axis is suppressed to form a convex receptacle. At the centre there is a single, long-stalked, naked pistillate flower, surrounding which there occur a large number of staminate flowers arranged in a scorpioid cyme. Each male flower consists of a single stamen, joined to a short stalk representing the pedicel, and arises in the axil of a hairy bracteole. The whole inflorescence is surrounded by an involucre of bracts, united to form a cup-like structure, with one or two nectar glands or without these. The order of development of flowers in this case is from inside outwards, i.e., *centrifugal*.

COMPARISON BETWEEN RACEMOSE AND CYMOSE INFLORESCENCES

The cymose inflorescence is definitely advanced than the racemose one so far as the mode of opening of the flowers is concerned. In the former case, new flowers open one after the other, in a centrifugal manner, and consequently, the fertilized ovaries (fruits) remain protected amongst the older parts. On the other hand, in the racemose type, the flowers usually open simultaneously in a centripetal manner, so that the fruits practically lie exposed. Moreover, there are other disadvantages of simultaneous flowering. Firstly, the insect visitors may fail to visit the flowers in due time for pollination, or the flowering period may be unsuitable for successful fertilization. Secondly, if

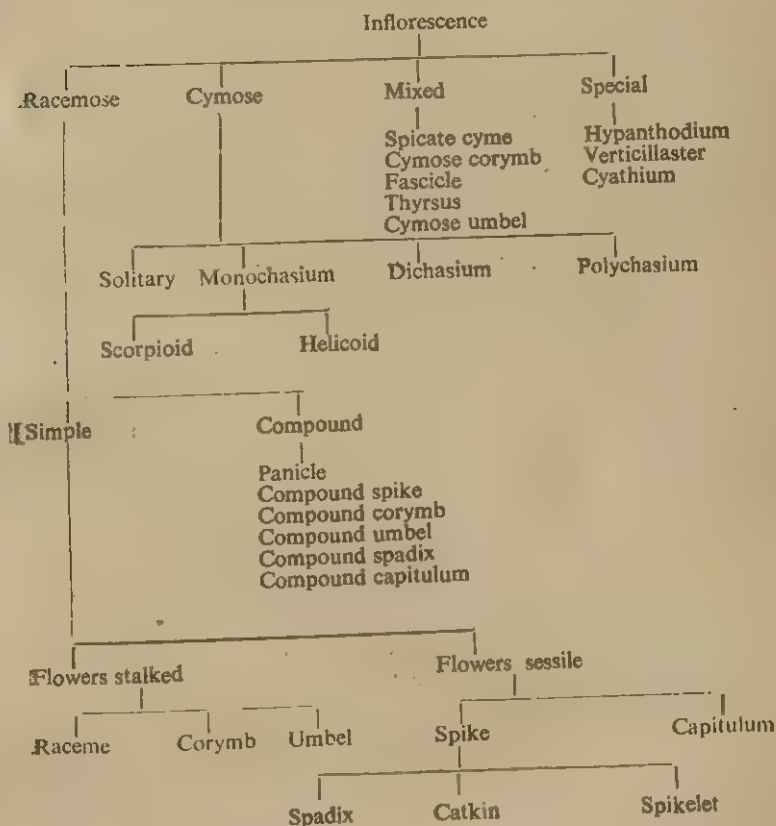
the growing apices of young racemosely-flowering shoots be accidentally destroyed, quite a large number of flowers will be lost thereby, and the capacity of new flower-production will be stopped. While, in the case of cymosely-flowering shoots, the chances of pollination and consequent fertilization are very highly secured, and if their growing apices be destroyed, these will suffer the loss of single flowers only, and very shortly the lateral branches below the injured apices will start flowering vigorously. It may be noted, however, that capitulum, though a racemose type of inflorescence, is more successful than the ordinary cymose types of inflorescence, since better protection of seeds is afforded, and a single insect can pollinate a number of flowers within a very short time.

EVOLUTION OF INFLORESCENCE

Three theories have been put forward to indicate the proposed line of evolution of the modern inflorescences from a hypothetical primitive type. According to workers, like Nägeli (1883), Celakovsky (1892), Pilger (1922), and others, the primitive type was a panicle. Goebel (1931) also accepted this view. The second theory, strongly supported by Parkin (1914), regards a solitary terminal flower as the most primitive. It is believed that by axillary growth, later on, lateral flowers as well as branches bearing flowers have been added, thus giving rise to a many-flowered inflorescence. If, it is accepted, however, that the flower as well as the foliar organs are extremely modified branch systems, the majority of the present-day cases of solitary flowers should have to be regarded as reduced and suppressed. In a third theory, Rickett (1944) accepted the idea that the dichasium was the primitive type, which, by slight structural changes, and by apparent suppression of internodes, had produced the various types of inflorescence. Rickett believes that in the simplest form of the primitive dichasium there were three flowers on a single peduncle, a terminal one and a pair of lateral ones immediately below it. From this type a more complex type of dichasium might have been formed. In the absence of any clear palaeobotanical evidence, however, it is rather unsafe to make any comment on the relative primitiveness of the simple and compound dichasia. On the basis of this theory, it is clear that the more complex and aggregated types of inflo-

Inflorescence indicate a possible line of development from a variety of aggregations and combinations of dichasia. Consequently, the apparently simple raceme and spike types are, in reality, reduced ones, which might have arisen by the reduction of individual dichasium to a single flower.

The inflorescence may be tabulated as follows :



CHAPTER VII

POLLINATION

Prior to the fertilization of the ovule and its subsequent transformation into a seed, pollen grains must be deposited on the receptive part or the stigma of the carpel. This transference of pollen grains from anthers to the stigma of the carpel of a flower is called **pollination**. In case of gymnosperms, the pollen grains are directly transferred to the open micropyles of the naked ovules. Pollination is of wide-spread occurrence in nature, and is responsible for the production of innumerable varieties of plants. There are two methods of pollination : (a) **self-pollination** or **autogamy** or **homogamy**, and (b) **cross-pollination** or **allogamy**. In the former case, the pollen grains from the anthers of a bisexual flower are transferred to the stigma of the same flower. The process may be either *direct* (i.e., when pollination takes place simply as a result of the relative position of the anther and the stigma), or *indirect* (i.e., when pollination takes place through the influence of some external agents, such as wind, insect, *etc.*). On the other hand, we speak of cross-pollination, when the pollen grains of one flower (unisexual or bisexual) are conveyed to the stigma of another flower, borne either on the same inflorescence or on the same plant (**geitonogamy**) or on different plants (**xenogamy**). All cases of cross-pollination are effected by some external agents. **Hybridization** or **hybridism** is a special type of cross-pollination usually brought about by human agency for the purpose of rearing up better plants.

CROSS-POLLINATION*

Cross-pollination is a case of normal occurrence in bisexual flowers, while it is a necessity in unisexual flowers.

The many contrivances, which are favourable for cross-pollination, are as follows :

* From a rigid biological standpoint, the term *cross-pollination*, however, should be applied to those cases only, where genetic constitutions of the two flowers involved in the process are entirely different (*vide* Vol. II, Part I).

DICLINY OR UNISEXUALITY

Sometimes stamens and carpels do not occur in the same flower, as such, the flowers are said to be **unisexual** or **diclinous**. In such cases, cross-pollination is inevitable. The types of dicliny noted in plants are : (a) **monoecism**, where both the male and female flowers are borne upon the same plant, as in most of the plants belonging to Fam. Euphorbiaceae, gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, maize (*Zea mays*) of Fam. Gramineae, palmyra palm (*Borassus flabellifer*) and betel-nut palm (*Areca catechu*) of Fam. Palmae, etc., and (b) **dioecism**, where male and female flowers are borne upon different plants of the same species, as in palwal (*Trichosanthes dioica*) and *Bryonia dioica* of Fam. Cucurbitaceae, papaw (*Carica papaya*) of Fam. Caricaceae, mulberry (*Morus indica*) of Fam. Moraceae, date (*Phoenix sylvestris*) of Fam. Palmae, etc.

SELF-STERILITY OR INCOMPATIBILITY

Sometimes, the pollen of a flower is completely ineffective, when it falls upon the stigma of the same flower, as in *Reseda odorata* (Fam. Resedaceae), some members of the family Solanaceae, a few fruit trees belonging to the family Rosaceae, etc. In some orchids, the pollen appears to possess a toxic and withering effect on the stigma of the same flower, while it is quite potent on the stigmas of other flowers of the same species.

DICHOGAMY AND CHASMOGAMY

The most common floral feature, that facilitates cross-pollination and makes self-pollination practically impossible in bisexual flowers, is **dichogamy**, a condition when the anthers and the stigmas mature at different times. There are obviously two possible cases of dichogamy : (a) **protandry** or **proterandry**, when the stamens mature first and the pollens may be shed before the stigmas are mature, as in most of the flowers of the families Malvaceae, Geraniaceae, Umbelliferae, Rubiaceae, Compositae, Labiatae, etc., and (b) **protogyny** or **proterogyny**, when the stigmas ripen first, before the pollen is ready to be shed, as in *Michelia champaca* and *Magnolia grandiflora* of Fam. Magnoliaceae, *Poinsettia pulcherrima* and *Pedilanthus tithymaloides* of Fam. Euphorbiaceae, *Adhatoda vasica* of Fam. Acanthaceae, etc.

In some cases, the flowers are bisexual and open (**chasmogamous**), and though the anthers and the stigmas mature simultaneously, yet self-pollination is made impossible due to certain facts discussed below.

(a) **Herkogamy.** Herkogamous flowers usually possess some special contrivances, which prevent self-pollination : (i) in *Clerodendrum* (= *Clerodendron*) *infortunatum* (Fam. Verbenaceae), the style moves away from the stamens, so that the pollen cannot fall upon the stigma of the same flower ; (ii) in many cruciferous plants, the anthers are situated at a lower level than the stigmas ; (iii) in some members of the family Caryophyllaceae, the stigma is furthest away from the anthers ; (iv) in glory lily (*Gloriosa superba*) of Fam. Liliaceae, the dehiscent face of the anthers is extrorse ; (v) the peculiar construction of the flowers, as in *Aristolochia indica* (Fam. Aristolochiaceae), and (vi) flowers possessing pollinia, as in *Calotropis procera* (Fam. Asclepiadaceae) and orchids (Fam. Orchidaceae) render self-pollination a mechanical impossibility.

(b) **Heteromorphism.** Sometimes, these flowers are borne upon different plants and possess styles of different lengths (**heterostyly**). Such flowers, obviously, have stamens of different lengths as well (**heteranthy**).

Heterostylic flowers are usually either **dimorphic** (i.e., with two different forms of flowers, one having long stamens and a short

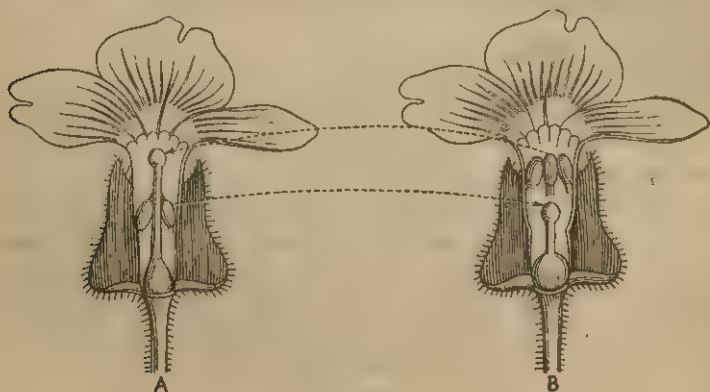


FIG. 133. DIMORPHIC FLOWERS OF *Primula*

style, and the other having short stamens and a long style), as in *Biophytum sensitivum* (Fam. Oxalidaceae), *Polygonum*

orientale and buck-wheat (*Fagopyrum esculentum*) of Fam. Polygonaceae, primrose (*Primula sinensis*) of Fam. Primulaceae (Fig. 133), beet (*Beta vulgaris*) of Fam. Chenopodiaceae, jasmine

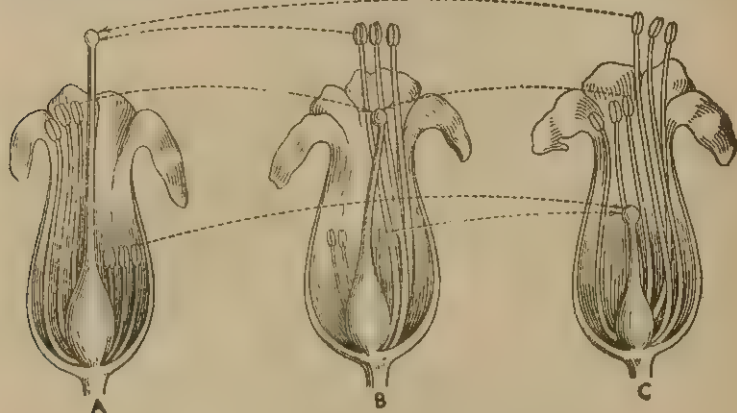


FIG. 134. TRIMORPHIC FLOWERS OF *Lythrum*

(*Jasminum* sp.) of Fam. Oleaceae, and in some members of the families Boraginaceae, Rubiaceae, etc., or **trimorphic** (i.e., with three different forms of flowers having short, long and medium stamens and styles), as in wood-sorrel (*Oxalis corniculata*) and carambola (*Averrhoa carambola*) of Fam. Oxalidaceae, *Woodfordia floribunda* and *Lythrum salicaria* of Fam. Lythraceae (Fig. 134), etc.

SELF-POLLINATION

Self-pollination takes place only in bisexual flowers and never in unisexual ones, and it occurs only when cross-pollination fails, excepting in a very few cases, where normal self-pollination is the rule.

The main contrivances which appear to be favourable for self-pollination are as follows :

HOMOGAMY

In many bisexual flowers, anthers and stigmas mature at the same time, and this leads to effective self-pollination. Further, there are flowers which are dichogamous but not completely

so, there being a short period during which self-pollination is possible.

Though chasmogamous flowers are, as a rule, cross-pollinated, yet, when cross-pollination fails in them, self-pollination may take place in the following ways :

(a) In flowers of *Clerodendrum* (= *Clerodendron*) *infortunatum* (Fam. Verbenaceae), marvel of Peru (*Mirabilis jalapa*) of Fam. Nyctaginaceae, etc., the filaments and the styles get spirally coiled ; (b) in sunflower (*Helianthus annuus*) of Fam. Compositae, the stigma curls back to reach the anthers ; (c) in Mexican poppy (*Argemone mexicana*) of Fam. Papaveraceae, the pollen grains, shed on the cup of the corolla, are brought in contact with the stigma by the closing up of petals ; (d) in prickly pear (*Opuntia dillenii*) of Fam. Cactaceae and in several members of the family Compositae, the filaments, which are somewhat inwardly curved from the very beginning, curve still further later on, until the anthers come to such a position that the pollen grains, when shed, fall directly upon the stigma ; (e) in many members of Fam. Cruciferae having protogynous flowers, the filaments of the shorter stamens elongate so as to bring the anthers to the level of the stigma ; (f) sometimes, the style elongates to receive the pollen, as in *Gardenia florida* (Fam. Rubiaceae) ; (g) in cases of *Grewia asiatica* (Fam. Tiliaceae) and some members of Fam. Malvaceae, the stigmas either bend or contract in order to come in close contact with the anthers.

In some heteromorphic flowers, where the stamens are situated at a higher level than the stigmas, the pollen grains may directly fall upon them and bring about self-pollination.

CLEISTOGAMY

There are some plants, which produce small and closed hermaphrodite flowers, in addition to the normal ones. These small flowers remain either on or under the ground and never open, so that self-pollination is inevitable. Such flowers are said to be **cleistogamous** ones or **cleistogenes**, as in *Commelina benghalensis* (Fam. Commelinaceae), balsam (*Impatiens balsamina*) of Fam. Bal-

* The majority of such flowers are **chasmocleistogamous**, because some of the hermaphrodite flowers are chasmogamous, while the others are cleistogamous.

saminaceae, pansy (*Viola tricolor*) of Fam. Violaceae, *Polygala polygama* (Fam. Polygalaceae), etc. In cleistogamous flowers, the walls of the anther lobes are so thin that, when the pollen grains actually germinate within the anthers, the pollen tubes pierce the wall of the anther and reach the stigma. *Polycarpon tetraphyllum* (Fam. Caryophyllaceae) has cleistogamous flowers only. Cleistogamy may be of two kinds : (a) **habitual or obligate cleistogamy**, when the flowers are typically cleistogamous and never open ; (b) **pseudo- or facultative cleistogamy**, when the flowers remain open for a very short time, and then close up permanently, as in wood-sorrel (*Oxalis corniculata*) of Fam. Oxalidaceae, *Portulaca oleracea* (Fam. Portulacaceae), sundew (*Drosera burmanni*) of Fam. Droseraceae, etc.

Besides being autogamous and allogamous, plants may be heterogamous as well, where individual plants differ so far as their pollination methods are concerned. Such heterogamous plants may be (i) **allo-autogamous**, when some of the individuals in a species are decidedly autogamous, while others are invariably allogamous, e.g., pansy (*Viola tricolor*) of Fam. Violaceae, (ii) **homodichogamous**, when some of the individuals are autogamous, others being distinctly dichogamous, e.g., bugloss (*Ajuga* sp.) of Fam. Labiatae, and (iii) **heterodichogamous**, when the individuals are protandrous in some cases and protogynous in others, e.g., walnut (*Juglans regia*) of Fam. Juglandaceae.

FLOWERS IN RELATION TO POLLINATING AGENTS

As pollination is effected, in the majority of cases, through various agencies, such as wind, water and animals, the types of pollination may be classified accordingly into : (a) **anemogamy** or **anemophily** (wind-pollination), (b) **hydrogamy** or **hydrophily** (water-pollination), and (c) **zoogamy** or **zoidiophily** (animal pollination), which includes (1) **entomogamy** or **entomophily***, where the insects are the pollinating agents, (2) **malacogamy** or **mala-cophily**, where slugs and snails bring about pollination, (3) **ornithogamy** or **ornithophily**, where pollination is caused by birds,

* A special terminology '**cantharogamy** or **cantharophily**' is attributed in case of pollinations brought about by beetles.

and (4) **chiropterigamy** or **chiropteriphily**, where bats are responsible for causing pollination.

ANEMOGAMY OR ANEMOPHILY

Anemogamous (anemophilous) or wind-pollinated flowers exhibit some common characteristics, which stand in definite relation to wind-pollination and cannot be regarded as merely accidental. Wind-pollinated flowers lack showiness, odour and nectar. These are usually inconspicuous, and either possess a simple perianth or are naked. In many cases, as in oak (*Quercus* sp.), birch (*Betula* sp.) and other plants of Fam. Cupuliferae, willow (*Salix tetrasperma*) and other plants of Fam. Salicaceae, *Trewia nudiflora* (Fam. Euphorbiaceae), etc., the staminate flowers are arranged in catkins, which are slender, pendulous inflorescences that swing freely in breeze, and the stamens are so oriented that after the anther lobes have opened, the pollens can be readily carried by the wind. Further, in most of these plants, the flowers develop before the leaves, thus facilitating exposure to wind. The staminate flowers of conifers are also similar. The mode of attachment of the versatile anthers in Fam. Gramineae on long slender filaments has the same significance.

In most wind-pollinated flowers, the pollen is produced in great abundance ; this is a matter of much advantage in view of the great waste. Thus, during seasons when the conifers are in flowers, large quantities of pollen fall to the ground, constituting what are known as 'sulphur showers'. Wind-scattered pollen is commonly smooth, light, and hence, easily blown about, and in the pines dispersal is facilitated further by the presence of wings. The pollen grains are not easily wetted ; this is highly advantageous, since moistening might prevent wind-dispersal and lead to premature germination.

The stigmas of the pistillate flowers, which catch the pollens are strongly developed and usually provided with long feathery or brush-like structures. In many gymnosperms, the micropyle of the megasporangium secretes a drop of fluid (**pollination drop**) in which the pollen grains are caught.

Many and perhaps most of the wind-pollinated flowers are **diclinous**, and in these, of course, there can be no **autogamy**. The majority of diclinous flowers are **monoecious**, and a few

are dioecious. The grasses (Fam. Gramineae), sedges (Fam. Cyperaceae), dock (*Rumex vesicarius*) of Fam. Polygonaceae, and plants belonging to Fams. Palmae, Chenopodiaceae, etc., are familiar examples of wind-pollinated flowers.

HYDROGAMY OR HYDROPHILY

Pollination through the agency of water is a relatively rare occurrence, but it is of much interest. It may occur beneath the water, or at its surface. In the former case, pollens are almost as heavy as water, and on being released go down the surface, as in many Potamogetonaceae, and *Ceratophyllum* sp. (Fam. Ceratophyllaceae). But, in the other case, where pollination occurs at the surface, the pollens are lighter than water, and, on being released, are carried on floats formed by the staminate flowers, as in *Vallisneria spiralis* (Fam. Hydrocharitaceae).

ENTOMOGAMY OR ENTOMOPHILY

The great majority of phanerogams are dependent upon the insects for the transference of their pollens. The most noticeable feature of insect-pollinated flowers is their showiness, which is due to their colour or to their size, position and arrangement. Some of them are fragrant and may also possess nectar. The inconspicuous flowers are frequently made conspicuous by coloured bracts, as in *Bougainvillea spectabilis* (Fam. Nyctaginaceae), *Poinsettia pulcherrima* (Fam. Euphorbiaceae), etc. In some cases, the stamens are modified into brightly coloured staminodes, as in most plants of the Order Scitamineae. Sometimes, corona and other appendages are developed, thereby rendering the flowers more attractive to the insects; in some cases, small inconspicuous flowers are made conspicuous by being aggregated together forming a head, as in *Anthocephalus cadamba* (Fam. Rubiaceae), sunflower (*Helianthus annuus*) and other plants of Fam. Compositae, candytuft (*Iberis odorata*) of Fam. Cruciferae, etc. Next to colour, odour is the most important factor for the allurements of insects. Usually, those flowers, such as *Cestrum nocturnum* (Fam. Solanaceae), different species of jasmine (Fam. Oleaceae), etc., which open at night, possess strong odour, since colour is of no importance at that time. The insects, thus allured by colour or odour, or both, are offered food in the form of pollen (e.g., potato,

lotus, poppy, etc.), or nectar secreted by the **nectaries**, present in different parts of flowers. The nectar is usually concealed, either in the corolla tube, as in *Datura metel* (Fam. Solanaceae), *Nerium peruvianum* (= *N. odorum*) of Fam. Apocynaceae, *Ipomoea pulchella* (Fam. Convolvulaceae), etc., or inside long spurs, as in *Impatiens balsamina* of Fam. Balsaminaceae, as well as in a large number of members belonging to Fam. Orchidaceae, etc. In some cases, in order that nectar may be found easily by the insects, the petals are often marked with coloured spots, or lines or grooves, called **nectar guides**. Sometimes, the visit of the insects is facilitated by the provision of the seat or alighting platform, in the form of the wings and the keel of many Leguminosae, the labellum or lip of Orchidaceae, Musaceae, Zingiberaceae, Marantaceae, Cannaceae, Labiatae, some Scrophulariaceae, and Acanthaceae. The platforms are generally provided in such a manner, that the proper insect visitors can readily touch either the anthers or the stigmas.

The stamens of insect-pollinated flowers are rarely exerted, and the filaments are often short. The pollens, instead of being dry and powdery, are normally adhesive through the possession of spines and other protuberances or sticky substances, so that these adhere easily to the body of the insect visitors.

The stigmas are short, rough and sticky, so that they can easily catch rough or sticky pollens.

The majority of insect-pollinated flowers are bisexual though a few are unisexual.

Depending on the nature of the insect visitors, the entomogamous flowers may be arranged into the following groups :

(a) Pollen flowers

Flowers like potato (*Solanum tuberosum*) of Fam. Solanaceae, lotus (*Nelumbo nucifera*=*Nelumbium speciosum*) and water lily (*Nymphaea lotus*) of Fam. Nymphaeaceae, poppy (*Papaver somniferum*) and *Argemone mexicana* of Fam. Papaveraceae, pomegranate (*Punica granatum*) of Fam. Punicaceae, *Michelia champaca* and *Magnolia grandiflora* of Fam. Mangoliaceae, *Anona squamosa* of Fam. Anonaceae, etc., have no honey but possess abundant pollen to offer as food to the insect visitors.

(b) Honey flowers

These flowers contain sufficient quantity of nectar to be utilized as food by the insects. According to the nature and construction of these flowers, and the position of nectar glands, the honey flowers may be :

(i) **Fly flowers.** These flowers are either very short-tubed as in bedstraw (*Galium* sp.) of Fam. Rubiaceae ; or shallow and open, as in stonecrop (*Sedum* sp.) of Fam. Crassulaceae, and many saxifrages (Fam. Saxifragaceae), etc. ; or contain nectar superficially, as in some Euphorbiaceae and most of the Umbelliferae. These are usually visited by flies and short-tongued beetles. Some fly flowers, like strawberry (*Fragaria vesca*) of Fam. Rosaceae, Indian buttercup (*Ranunculus sceleratus*) of Fam. Ranunculaceae, some Compositae, etc., with partly-concealed nectar, are frequented by longer-tongued beetles and flies, while the longest-tongued flies (chiefly hoverflies) visit medium-tubed flowers like blackberry (*Rubus* sp.) and gooseberry (*Ribes* sp.) of Fam. Rosaceae, *Geranium* sp. (Fam. Geraniaceae), etc.

(ii) **Bee flowers.** These are usually long-tubed (6-15 mm.) flowers and are chiefly visited by the larger bees, thus completely excluding the short-tongued flies and beetles. The flowers are zygomorphic and usually coloured blue, purple or red. The familiar examples of bee-flowers are snap-dragon (*Antirrhinum majus*) of Fam. Scrophulariaceae, larkspur (*Delphinium ajacis*) and monk's hood (*Aconitum napellus*) of Fam. Ranunculaceae, most of the Papilionaceae, Labiatae, Orchidaceae, Violaceae, *Pedilanthus tithymaloides* (Fam. Euphorbiaceae), goldfussia (*Strobilanthes* sp.) of Fam. Acanthaceae, etc. The flowers are occasionally visited by butterflies and moths.

(iii) **Butterfly and moth flowers.** In these flowers, the nectar is concealed almost at the bottom of the very long corolla-tube (2-30 cm.), and is beyond the reach of even the longest-tongued bees. The butterfly flowers are usually bright-red or blue. The familiar examples are pink (*Dianthus chinensis*) of Fam. Caryophyllaceae, *Ixora coccinea* (Fam. Rubiaceae), *Vitex negundo* (Fam. Verbenaceae), oleander (*Nerium peruvianum* = *N. odorum*) of Fam. Apocynaceae, glory lily (*Gloriosa superba*) of Fam. Liliaceae, *Ipomoea* sp. (Fam. Convolvulaceae), etc. The moth flowers are pale-yellow or white, without any nectar-

guides, and emit their scent in the evening. The common moth flowers are tuberoso (*Polianthes tuberosa*) of Fam. Amaryllidaceae, *Petunia* sp. and *Cestrum nocturnum* of Fam. Solanaceae, *Nyctanthes arbor-tristis** and jasmine (*Jasminum* sp.) of Fam. Oleaceae, etc.

MECHANISM OF POLLINATION IN A FEW COMMON PLANTS

(1) GARDEN PEA (*Lathyrus odoratus*, Fig. 135) of S.F. Papilionaceae (Fam. Leguminosae).

The flowers of the common garden pea are variously coloured and sweet-scented. These are usually bee-pollinated. The vexillum acts as an advertiser, and the alae are the resting places for the bees. These perform the functions of levers in depressing the keel, when a bee visits the flower in quest of nectar concealed at its base. By the depression of the keel, the anthers and the stigma, so long hidden within, are jerked out and come in contact with the ventral surface of the visitor, thereby dusting its body with pollen grains. As soon as the insect departs, the pressure on the keel is released, and the stamens and the stigma swing back to their original positions. Next, when the bee visits another



FIG. 135. POLLINATION IN GARDEN PEA.

A bee is going to alight on the alae.

flower, some of the pollens from its body get stuck to the stigma, and thus pollination is effected. The visitor not only does pollinate the second flower, but also receives a fresh crop of pollen in return.

(2) GARDEN SAGE (*Salvia plebeja*, Fig. 136) of Fam. Labiatae.

The flowers of the garden sage are typically protandrous and bee-pollinated. These have a bilabiate corolla, which is tubular below. The lower lip of the corolla is conspicuously attractive and serves as the landing stage for the bees, while the upper lip simply protects the stamens and the gynaecium. There are only two fertile

* Shaw (1952) has placed this plant under Fam. Verbenaceae.

stamens, the other two being represented by staminodes. Each stamen has a short filament (the basal portion of which is fixed), which is joined to a long curved connective with two arms of unequal lengths, which act as a lever. The short arm of the connective is sterile, while the longer one bears a fertile anther, and this remains hidden within the upper lip of the corolla. When a bee (searching for nectar) alights upon the lower lip and

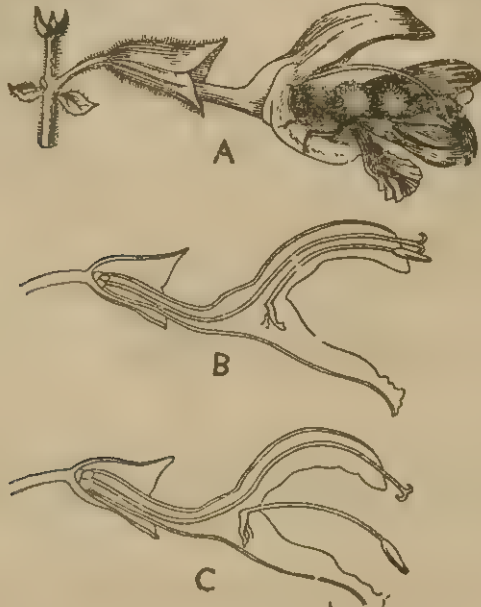


FIG. 136. POLLINATION IN GARDEN SAGE

A, a bee has entered into a flower ; B, l.s. of the flower showing the position of the lever before the entrance of the bee ; C, the same after entrance of the bee.

pushes its head inside the corolla-tube, it (the head) gives a pressure to the short arm of the lever. With the depression of the shorter arm, the basal part of the filament, which serves as a fulcrum, is disturbed ; the longer arm bearing the fertile and mature half-anther swings out of the upper lip, comes in contact with the bee's back, and thereby dusts its body with pollen grains. The bee, thus laden with pollen grains, next visits a second flower, in which the gynaecium has been matured by this time and the style has already elongated to a certain extent ; its stigma comes

in contact with the pollen-dusted back of the insect, and catches hold of some of the pollens. Thus the pollination is effected.

(3) FIG (*Ficus carica*, Fig. 137) of Fam. Moraceae.

The pollination in this case is brought about by a particular kind of wasp. The inflorescence (hypanthodium) is very peculiar

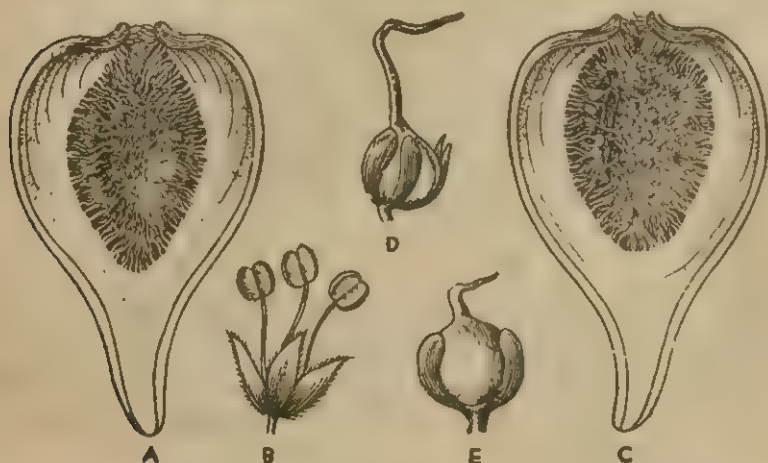


FIG. 137. POLLINATION IN FIG

A, l.s. of a hypanthodium showing pistillate flowers ; B, a staminate flower ; C, l.s. of a hypanthodium showing staminate and short-styled pistillate flowers ; D, a long-styled pistillate flower ; E, a short-styled pistillate flower producing a gall.

being more or less jug-shaped in outline with a minute apical opening, and contains numerous unisexual flowers. The staminate flowers are situated near about the apical pore, while the pistillate ones are placed deeper down the hollow cavity of the jug ; these latter ones are either short-styled or long-styled. A female wasp ordinarily creeps through the pore of the jug into its interior, and lays eggs inside the ovaries of the short-styled pistillate flowers (**gall flowers**). The larvae, developing from the eggs, derive their nourishment from the tissues of the ovary, ultimately destroy the ovules and convert the ovary into a gall. Finally, when the mature and adult wasp comes out of the fig, its body brushes against the staminate flowers and becomes dusted with the pollen grains. When it next visits another inflorescence containing long-styled female flowers, the pollens are deposited on their stigmas. The styles of these flowers are so very long that the eggs of the wasps

cannot reach the ovary of the flowers, and hence fail to develop. As such, gall-formation is unknown in the inflorescence with long-styled flowers; normal seeds are produced in great abundance there.

(4) ADAM'S NEEDLE (*Yucca* sp., Fig. 138) of Fam Liliaceae.

The flowers on the inflorescence axis of *Yucca* are white in colour, and remain in a drooping condition. At first, the anthers as well as the stigmatic surface remain enclosed by the perianth-lobes. At the time of pollination, which is brought about by a special type of moth, known as the yucca-moth, the perianth-lobes separate out and expose the projected stigma, which is much beyond the reach of the anthers, and thus self-pollination is avoided. The moth, coming in search of honey, carries masses of pollen grains in its coiled maxillary palp, and when it visits the next flower, it stuffs the pollen grains on the stigmatic surface. These grains are also utilized as food by the young larvae, hatched out of the eggs already laid within the ovary. It should be noted that after the pollination is over, the perianth-lobes close up once again.



FIG. 138. POLLINATION IN *Yucca*.

(5) ARISTOLOCHIA INDICA (Fig. 139) of Fam. Aristolochiaceae.

The protogynous flower of *Aristolochia* has a peculiar type of perianth, which is dilated below, constricted in the middle region forming a narrow tube, and once again obliquely spreading out in its upper part. The tube is provided with obliquely placed, downwardly directed hairs, which allow an easy entrance of small flies within the inflated portion of the perianth, but prevent their escape for the time being. It is only when the anthers mature and shed their pollen grains, and the hairs dry up and fall off forming a clear passage, that the pollen-laden flies can come out. When

A, an unopened flower; B, a mature flower with 3 of the perianth-lobes removed to show the presence of the moth inside.

these flies visit the next young flower, the pollen grains are deposited on the mature stigmatic surface, and thus cross-pollination is effected, but they themselves remain temporarily imprisoned once again awaiting the maturity of the anthers. It is to be noted that, after pollination, there is no further secretion of nectar within the flower, and the apical portion of the perianth droops down forming a lid, which prevents any further entrance of the flies.



FIG. 139
POLLINATION IN
Aristolochia.

A fly is shown within the inflated portion of the perianth.

(6) MADAR (*Calotropis procera*, Fig. 140) of Fam. Asclepiadaceae.

The flower of *Calotropis* is peculiarly constructed having the style united with the stigma forming a gynostemium, and the pollen grains are united together forming masses of pollinia. Two such pollinia, attached to a common gland (**retinaculum** or **corpusculum**) by means of two slender thread-like structures (**caudicles**), are situated at each corner of the pentangular stigmatic head, and remain covered by a membrane. When a bee visits a flower in quest of nectar, the pollinia get attached to its leg or proboscis with the help of the

retinaculum. At the time of its flight, the pollinia are dragged out forcibly, and when it visits another flower, these (pollinia) are deposited on the stigma. Thus the pollination is effected.

(7) ORCHID (Fam. Orchidaceae, Fig. 141).

The mode of construction of the flower of a common orchid is very intricate, and shows that even mature homogamous flowers favour cross-pollination. Here also the gynostemium is formed bearing two naked pollinia at its top, and just below them lies the rostellum concealing the stigmatic surface, formed



FIG. 140. POLLINATION
IN *Calotropis*.

by the fusion of two stigmatic lobes. Usually, a long-tongued bee brings about pollination. The visitor uses the brightly-coloured labellum as the landing stage, and tries to get nectar concealed in the nectar-containing spur. In its attempt to reach the source of nectar, it pushes back the rostellum and even breaks it, and thus the pollinia are liberated and get stuck to its forehead or leg with the help of sticky discs. These pollinia at first stand in an upright

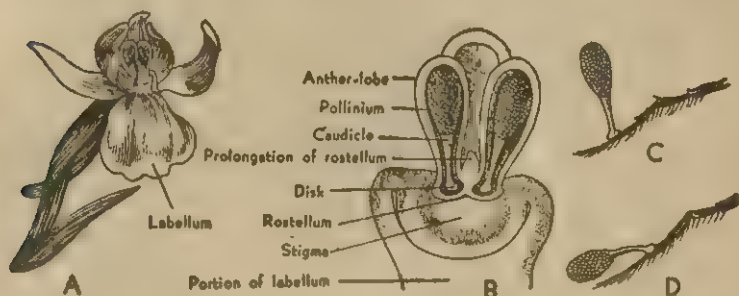


FIG. 141. POLLINATION IN ORCHID

A, an entire flower ; B, v.s. of the same after removal of the accessory whorls ; C-D, different positions of pollinia, while attached to the leg of bee.

position, but afterwards, when the insects visits another flower, the caudicle being flexible in nature bends down and help the pollinia to come in contact with the receptive surface of the stigma. Now the stigma, which is extremely viscid, catches hold of the pollinia very strongly, so that, when the bee flies away from the flower, at least a part of the pollinia, if not the entire mass, will remain adhering to the stigma. Thus the pollination is effected.

(8) TAPE GRASS (*Vallisneria spiralis*, Fig. 142) of Fam. Hydrocharitaceae.

The plant is a submerged, rooted, and aquatic dioecious one bearing tufts of ribbon-shaped leaves. The male plant bears minutely-stalked spathes enveloping many zygomorphic staminate flowers, while the female one bears a solitary, long, and spirally-stalked pistillate flower. At the time of pollination, the unopened staminate flowers become detached from the parent plant, and come up to the surface of water. Curiously enough, the pistillate flower also by this time uncoils its stalk, and rises to the surface.

The staminate flowers then open and exhibit their stamens, and while floating freely, come in contact with the pistillate ones. The two flowers are so arranged that as soon as the stamens touch

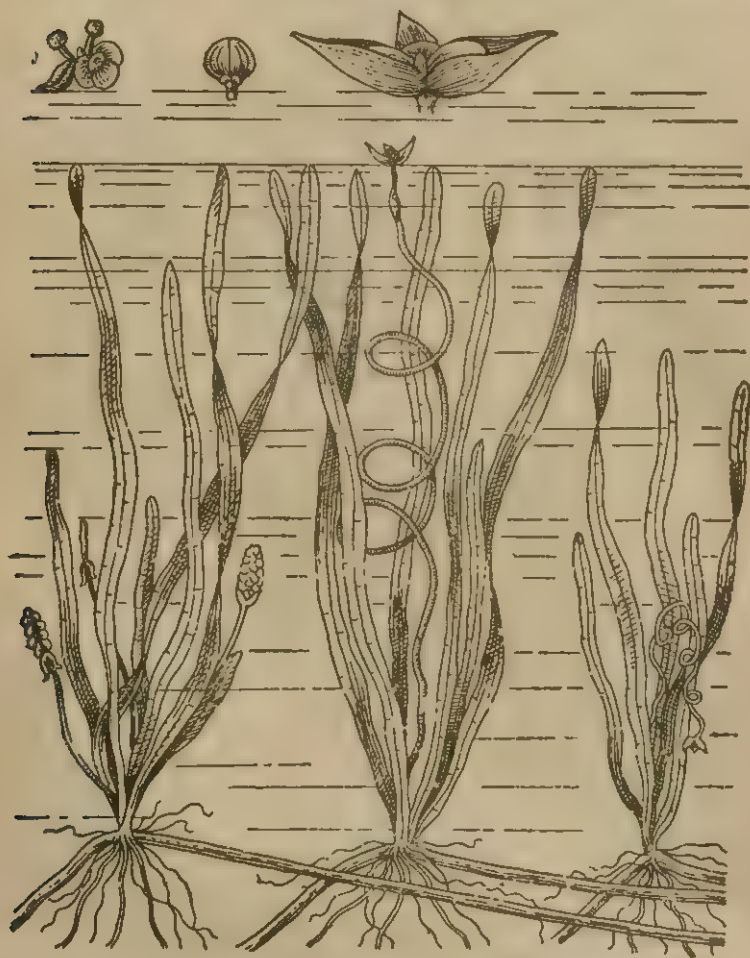


FIG. 142. POLLINATION IN *Vallisneria*

the stigma, the anthers dehisce, and a large mass of sticky pollen grains adhere to the surface of the stigma. After pollination, the pistillate flower goes down by the contraction of the spiral stalk, and further development takes place there.

ADVANTAGES AND DISADVANTAGES OF CROSS- AND SELF-POLLINATION

Although cross-pollination leads to the production of better seeds, or more seeds, than self-pollination, yet some plants produce quite as many seeds, and those of as good quality, by self-pollination. Cross-pollination has this advantage over self-pollination, that it frequently affords a better crop of seeds. But self-pollination is superior in one respect : it is easily secured and rendered certain ; the pollen simply has to come in contact with the stigma, which is ready and close at hand. The self-pollinated plant is not depended on the presence of another plant of the same kind in the immediate neighbourhood ; furthermore, it is never dependent upon any external agent to carry the pollen to another plant.

CHAPTER VIII

FERTILIZATION

It has already been stated that pollination is a necessary preliminary to **fertilization** or **syngamy** or **fecundation**, which means the act of union of two dissimilar sexual cells, male and female, called **gametes**. For fertilization of each ovule, at least one pollen grain is absolutely necessary, and for this reason there is always an abundance of pollen grains on the stigmatic surface. The process of fertilization in the angiosperms has been discussed below in a general way.

DEVELOPMENT OF THE POLLEN TUBE (MALE GAMETOPHYTE, Fig 144)

When the pollen grains reach the stigma, they adhere to its usually rough or papillate surface and begin to germinate (Fig. 143). This is facilitated by the secretion of a sugary fluid, the **stigma-**

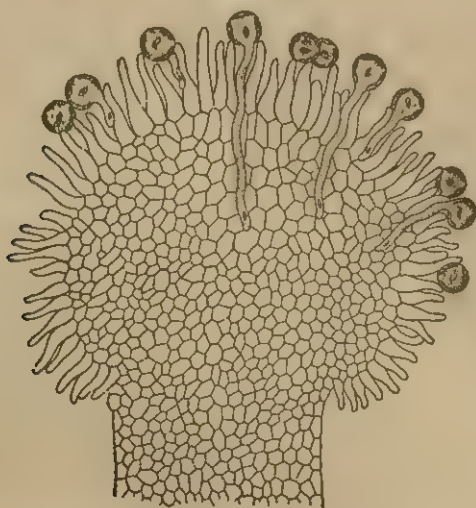


FIG. 143. GERMINATION OF POLLEN GRAINS ON THE STIGMA

tic fluid, from the stigma. Each pollen grain absorbs the stigmatic fluid, and, as a result, the inner wall or **intine** is stretched and extended through one of the thin areas or **germpores** in the **exine** in the form of a tube, called the **pollen tube**, which re-

presents the male gametophyte.* A pollen grain germinates only when it has become fully mature. Before germination, it increases considerably both in size as well as in volume ; a conspicuous central vacuole appears in the midst of the dense cytoplasm, thereby shifting the position of the nucleus from the central to a peripheral one. The first stage in the germination is marked by the formation of a small, nucleated cell lying against

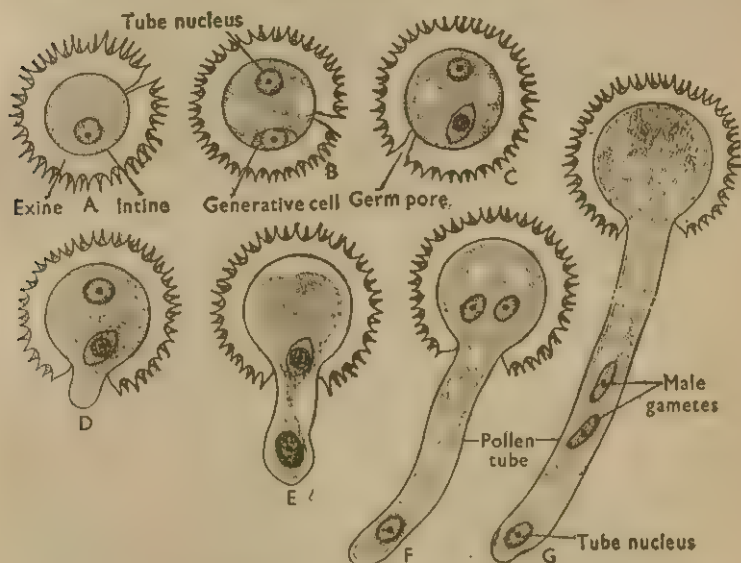


FIG. 144. GERMINATION OF THE POLLEN GRAIN AND DEVELOPMENT OF THE POLLEN TUBE.

the spore wall. This small cell, the **generative cell**, is separated from the rest of the large, naked cell, the **vegetative** or **tube cell**, by means of a distinct wall. Further, the nuclei of these two cells also differ from one another in size, structure and staining qualities ; the nucleus of the vegetative cell possesses a very prominent nucleolus, while, that of the generative cell may have a small one or none at all. Very soon, the generative cell gets itself detached from the spore wall, becomes fusiform or ellipsoid in shape, and remains embedded in the cytoplasm of the vegeta-

* Eames (1961), however, states that "the pollen tube is an extension of part of the inner layer of the spore wall ; it does not constitute 'the male gametophyte', even though it may enclose most of the male gametophyte."

tive cell. Subsequently, the generative cell divides and gives rise to two distinctly walled lenticular, ellipsoid, vermiform, or spherical cells (not naked nuclei, as previously believed), the **male gametes**. These two gametes are usually identical in shape and size, but, during their course of downward journey through the pollen tube, their shape may undergo some change. It should be noted, however, that this division of the generative cell may take place either within the original spore wall or within the pollen tube. The nucleus of the vegetative cell, commonly referred to as the **tube nucleus**, usually shows signs of degeneration with the maturation of the generative cell. Finally, it may remain within the spore wall, or may enter the pollen tube sooner or later, or even may be completely degenerated. It has, however, nothing to do with controlling the growth of the pollen tube, as was formerly suggested ; because, it has been noted in the case of the members of Fam. Amentiferae, that the pollen tube may branch repeatedly, and the branches, which do not possess any tube nucleus, grow equally well like that possessing it. The pollen tube, as it grows, gradually penetrates the tissues of the stigma and the style, and reaches the ovary. In the case of a hollow style, the entry is facilitated by the mucilaginous nature of the inner portion of the style, but in case of solid types, it is assisted by the presence of intercellular spaces as well as by the secretion of an enzyme from the tip of the pollen tube. This enzyme dissolves the stilar tissue, and the pollen tube advances through it. The food substances, such as proteids and fats, which are necessary for the growth of the pollen tube are mainly supplied by the grain itself. As the tube gradually elongates, the two male gametes, the tube nucleus and most of the cytoplasm remain near its tip.

The length of the pollen tube may be variable in different species. In some cases, it traverses a very short distance of only a few millimetres, while in others, as in maize (*Zea mays*) of Fam. Gramineae, it has to travel a distance of about 45 centimetres before it reaches the ovule. The span of time, which passes in between pollination and fertilization, varies from species to species, and it is governed by environmental conditions, as well as by the genetic constitutions of both the pollen and the stilar tissue. In autumn crocus (*Colchicum autumnale*) of Fam. Amryllidaceae, the pollen tube takes more than six months to traverse a distance

of only a few centimetres through the style, while in true crocus (*Crocus sativus*) of Fam. Iridaceae, though the distance to be traversed by the tube is 10 centimetres or more, yet the time taken is only 2 or 3 days. In some oaks (Fam. Cupuliferae), on the other hand, the tube takes almost a year to grow only 2 or 3 centimetres. This extremely slow development of the pollen tube is one of the very common causes of apparent sterility of the pollen.

When the delicate pollen tube reaches the ovary, it grows towards the micropyle of the ovule. On entering the ovary, it clings to its inner moist surface. When the pollen tube enters through the micropyle, the phenomenon is called **porogamy**. In certain types, it avoids the entry through the micropyle, but penetrates through the tissue of the basal or chalazal portion of the ovule, as in whip tree (*Casuarina equisetifolia*) of Fam. Casuarinaceae, *Juglans regia* (Fam. Juglandaceae), etc.; this phenomenon is known as **chalazogamy**.* In some cases, the pollen tube follows another route and enters into the ovule through its integument; this is called **mesogamy**.†

PROCESS OF FERTILIZATION (Fig. 145)

When the pollen tube enters the micropyle, it first comes in contact with the tissue of the nucellus. It then pierces this tissue and finally the wall of the embryo sac, and comes in the vicinity of the egg apparatus. What stimulus guides the tip of the pollen tube to the egg apparatus is not yet known; probably, it is guided by a chemotropic stimulus. However, the tip of the pollen tube passes through and destroys one of the synergids (rarely both), bursts and discharges its contents into the cavity of the embryo sac; subsequently, the affected synergid is destroyed. The nucleus of one of the two male gametes fuses with the egg. The other male nucleus fuses with the definitive nucleus of the embryo sac to form the **endosperm nucleus**. This phenomenon of twofold union is known as the **double fertilization**, the fusion between a sperm nucleus and the ovum only constituting **fertilization**. During the process, the tube nucleus either disappears from the pollen tube before the penetration of the wall of the embryo sac, or it

* Sometimes, also termed as **basigamy**.

† All other methods of entrance of the pollen tube, excepting porogamy, have been collectively termed as **apogamy** (Eames, 1961).

soon disorganises after its entry from the pollen tube into the cavity of the embryo sac. Each gamete, whether male or female, contains n number of chromosomes (*haploid*). As a result of

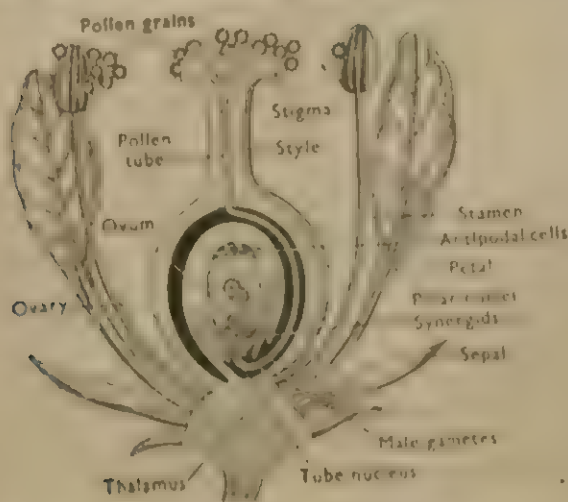


FIG. 145. LONGITUDINAL SECTION OF A FLOWER SHOWING THE PROCESS OF FERTILIZATION (Semi-diagrammatic).

fusion between the ovum and the sperm nucleus (each of which is a product of reduction division), a fusion nucleus is formed containing $2n$ number of chromosomes (*diploid*) so that the double number of chromosomes is restored. This fusion nucleus with its surrounding cytoplasm now becomes a zygote, called the **oospore** (which represents the sporophyte), after secreting a wall round itself. This zygote ultimately develops into the **embryo**.* It is already known that the definitive nucleus contains $2n$ number of chromosomes (products of union of two polar nuclei each having n number of chromosomes). When the second nucleus fuses with this nucleus, the so-called *triple fusion* results, and the resulting nucleus contains $3n$ number of chromosomes.

The fate of the antipodal cells may also vary in different species. In many species, these soon degenerate, while in others, the antipodals form some nutritive tissue until the endosperm is fully formed.

* For the development of the different types of embryo, refer to Part III.

FORMATION OF SEED AND FRUIT

The stimulus of fertilization causes a rapid growth of other tissues of the ovule along with the developing embryo and the endosperm. Owing to a rapid translocation of foods to the ovule in association with many physical and chemical changes, the ovule increases in size. The nature and thickness of its one or both integuments undergo considerable changes, and these frequently harden and dry up to form seed coats. The translocated reserve materials are converted within the seed into insoluble storage forms. The water content decreases, and the soft and succulent ovule is thus gradually changed into a relatively hard and dry body, the **seed**.^o During these physiological activities the fully developed embryo gradually passes into a state of dormancy. Thus, a seed is really a ripened ovule (*integumented megasporangium*), formed as a result of fertilization, containing a resting embryo with stored food and protected by seed coats. In some seeds, an outgrowth in the form of an investment develops from the funiculus or from the micropyle, which grows up and surrounds the seed either partially or wholly. This structure is known as the **aril**. It is usually fleshy, but may be otherwise. In nutmeg (*Myristica fragrans*) of Fam. Myristicaceae, it is developed both from the micropyle and the funiculus. Smaller outgrowths of this nature are called **caruncles**, formed either at the hilum, as in papyrus (*Cyrtus tricolor*) of Fam. Vioaceae, or at the micropyle as in castor (*Ricinus communis*) of Fam. Euphorbiaceae. Other lamellar examples of aril are litchi (*Litchi chinensis*, *Nephelium litchi*) and longan (*Nephelium longana*) of Fam. Sapindaceae, mangosteen (*Garcinia mangostana*) of Fam. Guttiferæ, etc.

Due to effect of fertilization†, usually the stamens, petals and sepals (together with the style and the stigma of the carpel)

[illegible]

parthenocarpic. *Parthenocarpic* (par'the-no-kar'pik) is an adjective meaning "bearing fruit without fertilization." *Parthenocarpic* (par'the-no-kar'pik) is an adjective meaning "bearing fruit without fertilization." *Parthenocarpic* (par'the-no-kar'pik) is an adjective meaning "bearing fruit without fertilization."

dry up and fall off, and the ovary is stimulated to a rapid growth. It greatly increases in size, and its tissues become highly differentiated resulting in the formation of a **fruit** containing the seed or seeds inside. In some cases, however, the receptacle, as in apple (*Pyrus malus*) and pear (*Pyrus communis*) of Fam. Rosaceae, or the calyx, as in *Dillenia indica* (Fam. Dilleniaceae), may also be stimulated to grow and take part in the formation of fruits. Thus, *the fruit is really a ripened ovary containing the seed or seeds, and in some cases, is together with other accessory structures, developed from the receptacle or the calyx.*

The formation of fruits and seeds is an exhaustive process during which usually the vegetative growth is arrested. In case of annuals, the plants die down soon after the formation of fruits and seeds, and these seeds are the only survivors for the perpetuation of the species.

In the following table the various parts of the flower which contribute to the formation of fruits and seeds are given :

| | | | | |
|--------------------------|----------------|---|----------------------------|--------------------------------------|
| Calyx | | Persistent (accrescent or marcescent) or deciduous | | |
| Corolla | | Usually deciduous | | |
| Androecium | | Usually deciduous | | |
| Gynaecium | { Stigma | Usually withers ; in some cases, remnants may be present | | |
| | { Style | Usually withers ; in some cases, remnants may be present | | |
| | { Ovarian wall | Fruit wall or pericarp, often differentiated into <div> <div>Exocarp</div> <div>Mesocarp</div> <div>Endocarp</div> </div> | | |
| Different parts of ovule | Ovary | { Placentae | Become variously modified | |
| | | { Ovule | Seed | |
| | { | Funiculus | Seed stalk or funiculus | |
| | | Raphe | Raphe | |
| | | Chalaza | Chalaza | |
| | | Micropyle | Micropyle | |
| | | Nucellus | Perisperm (rarely present) | |
| | { | Egg apparatus | { Synergids | Destroyed |
| | | | { Ovum (fertilized) | Embryo |
| | | Definitive nuclues (fertilized) | | Endosperm (may be present or absent) |
| | | Antipodal cells | | Usually disintegrate |

CHAPTER IX

THE FRUIT

It has already been stated that when fully ripe, the enlarged ovary containing one or more seeds is conventionally called a **fruit**, which is the product of a single ovary as a result of fertilization in the strictest sense of the term. But other floral parts, such as the receptacle and the calyx, may also be stimulated to grow and form a part of the fruit. A **true fruit** is the product of the carpel of a single flower having a superior ovary, as in mango (*Mangifera indica*) of Fam. Anacardiaceae, or an inferior one, as in guava (*Psidium guayava*) of Fam. Myrtaceae. A **false** or **spurious fruit**, on the other hand, is derived either from an inflorescence, or from a single flower, in which other floral parts and the axis may also take part in the formation of the fruit. Common examples of spurious fruits are sunflower, gourd, cucumber, *etc.* (derived from the inferior ovary, cup-like receptacle contributing to the formation of fruit) ; *Dillenia* (persistent accrescent calyx) ; apple, pear, *etc.* (mainly the fleshy receptacle) ; and jackfruit, pineapple, fig, mulberry (from the entire inflorescence).

The fruits have a wide range of construction. In general, the term **pericarp** is applied to the wall of the fruit, when it is derived solely from a superior or an inferior ovary. In many cases, the pericarp is thin and dry, but when thick and fleshy, it is usually differentiated into three regions (Fig. 146) : **exocarp**, or the outermost region, which is usually made up of a single layer of epidermal cells and varies in structure in different types of fruits ; **mesocarp**, which lies beneath the exocarp, constitutes the middle region of the fruit wall, and possesses the vascular bundles ; this region is usually more or less well-developed and juicy, or may be thin ; and **endocarp**, or the innermost region of the fruit wall, which either consists of a single layer of cells or

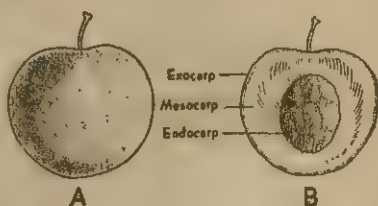


FIG. 146. PARTS OF PERICARP
A, an entire fruit of plum ; B, l.s.
of the same.

may be composed of several modified cellular layers, but sometimes, this region becomes hard and stony. The relative proportions of these regions are very variable in different types of fruits, and very often these cannot be distinguished from one another without the aid of a microscope. The gymnosperms among the flowering plants do not possess any fruit.

CLASSIFICATION OF FRUITS

Fruits are classified into three groups : *simple*, *aggregate* and *multiple* or *composite*.

A **simple fruit** is one, which is developed from a single flower with a monocarpellary or multicarpellary syncarpous gynaecium, while an **aggregate fruit** is the product of a single flower with multicarpellary apocarpous gynaecia. Here the ovary of each carpel gives rise to a separate fruit, called *fruitlet*, hence, an aggregation of fruitlets is formed over the single receptacle. On the other hand, a **multiple** or **composite fruit** is developed from an inflorescence. Here, the ovaries as well as other floral parts of several flowers more or less coalesce together forming a single mass.

SIMPLE FRUITS

The simple fruits, according to the consistency and structure of the pericarp and the modes of dehiscence, may be as follows :

I. DRY FRUITS

(Pericarp simple, dry, membranous, leathery or woody.)

A. INDEHISCENT FRUITS (not splitting open at maturity, usually one-seeded, and hence, known as **achenial fruits**). The chief types of indehiscent fruits (Fig. 147) are discussed below.

Achene. It is developed from a monocarpellary gynaecium with a superior, 1-chambered ovary, and the pericarp and the testa are free from each other, as in sorrel (*Rumex vesicarius*) of Fam. Polygonaceae, *Mirabilis jalapa* and other plants of Fam. Nyctaginaceae, etc. Usually, achenes occur in groups, hence, many aggregate fruits consist of collection of achenes, as in *Naravelia zeylanica*, *Clematis gouriana*, and fennel (*Nigella sativa*, Fig. 147, C) of Fam. Ranunculaceae.

Caryopsis. It is like achene, but the pericarp and the testa are inseparably fused together, as in wheat (*Triticum aestivum* = *T. vulgare*), maize (*Zea mays*, Fig. 147, B), paddy (*Oryza sativa*) and other plants of Fam. Gramineae.

Cypsella. It is developed from a bicarpellary syncarpous gynaecium with an inferior, 1-chambered ovary, as in sunflower (*Helianthus annuus*, Fig. 147, A), marigold (*Tagetes patula*) and other plants of Fam. Compositae. In many cases, it is crowned with a pappus, as in *Vernonia cinerea*, *Blumea lacera*, etc.

Nut. It is developed from a bi- or multi-carpellary, syncarpous gynaecium with a superior ovary, and the pericarp is woody or leathery, as in *Sapindus trifoliatus* (Fam. Sapindaceae), oak (*Quercus* sp., Fig. 147, D) of Fam. Cupuliferae, *Casuarina equiseti-*

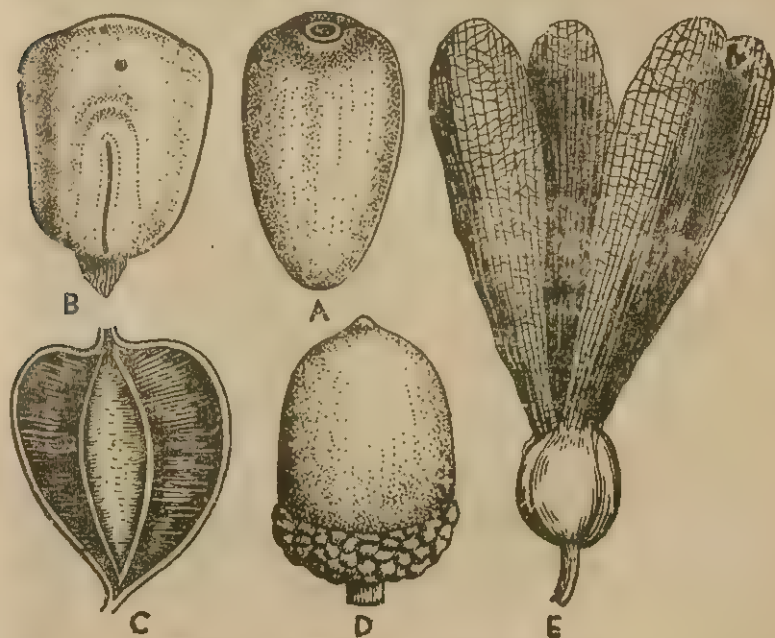


FIG. 147. INDEHISCENT (ACHENIAL) FRUITS

A, cypsella ; B, caryopsis ; C, achene ; D, nut ; E, samaraoid fruit.

folia (Fam. Casurinaceae), etc. Litchi (*Litchi chinensis* = *Nephelium litchi*) of Fam. Sapindaceae is also a nut with a fleshy aril lying between the pericarp and the seed.

Samara. It is a few-seeded fruit with the pericarp flattened into wings, developing from a multicarpellary gynaecium with a superior 2- or more-chambered ovary, as in *Hiptage madablota* (Fam. Malpighiaceae).

In some cases, the lobes of the persistent calyx develop into winged structures, the fruits remaining inside the enlarged calyx-tube but free from it, so that, the fruit is carried bodily by the wind. Such fruits are called **samaroid** ones. The ovary in these cases may be either superior, as in the genera *Ulmus* (Fam. Ulmaceae), *Dipterocarpus* and *Shorea* (Fig. 147, E) of Fam. Dipterocarpaceae, or inferior, as in *Combretum* (Fam. Combretaceae), etc.

B. DEHISCENT FRUITS (splitting open at maturity).

The chief types of dehiscent fruits (Fig. 148) are as follows :

Legume or pod. It is developed from a monocarpellary gynaecium with a superior, 1-chambered ovary, and splits up along both the sutures at maturity, as in pea (*Pisum sativum*, Fig. 148, A and B), lablab (*Dolichos lablab*) and other plants of S.F. Papilionaceae (Fam. Leguminosae).

Follicle. It is developed from a syncarpous gynaecium where the union among the carpels is very slight and restricted to the upper or lower part only and splits up along the ventral suture alone. In the Fam. Asclepiadaceae (Fig. 148, C), follicles are derived from the two ovaries of an apocarpous gynaecium, each forming a separate fruitlet dehiscing by the ventral suture. Other familiar examples may be found in monk's hood (*Aconitum napellus*), columbine (*Aquilegia vulgaris*) and a few other plants of Fam. Ranunculaceae, *Sterculia foetida* and some other plants of Fam. Sterculiaceae, *Aganosma caryophyllata*, *Vinca rosea* and some other plants of Fam. Apocynaceae, etc.

Siliqua. It is developed from a bicarpellary syncarpous gynaecium with a superior, falsely 2-chambered ovary, and splits up from the base to the apex leaving the seeds attached to the replum, as in mustard (*Brassica nigra*, Fig. 148, D & E), radish (*Raphanus sativus*) and the majority of plants of Fam. Cruciferae.

Silicula. It is short, wide and few-seeded siliqua, as in shepherd's purse (*Capsella bursa-pastoris*) and candytuft (*Iberis odorata*) of Fam. Cruciferae.



FIG. 148. DEHISCENT FRUITS

A-B, legume ; C, follicle ; D-E, siliqua ; F-G, capsule.

Capsule. It is developed from a bi- or multi-carpellary gynaecium, with a superior (sometimes inferior) ovary, and opens by valves or pores, as in cotton (*Gossypium herbaceum*), lady's finger (*Hibiscus esculentus*, Fig. 148, F & G) of Fam. Malvaceae, thorn apple (*Datura fastuosa*) of Fam. Solanaceae, etc.

The capsular fruits may open in one of the following ways :

(a) *Septicidal*, when splitting into component carpels along their lines of union, so that the placentae separate in the middle, as in castor (*Ricinus communis*, Fig 149, B) of Fam. Euphorbiaceae, linseed (*Linum usitatissimum*) of Fam. Linaceae, etc.

(b) *Loculicidal*, when the splitting takes place along the middle of each carpel, so that each half, thus formed, consists of the adjoining halves of two carpels, and the placentae are found along the united margins of these halves, as in cotton (*Gossypium herbaceum*, Fig. 149, C) of Fam. Malvaceae, *Adhatoda vasica*, *Andrographis paniculata* and other plants of Fam. Acanthaceae, etc.

(c) *Septifragal*, when splitting takes place either in the loculicidal or in the septicidal manner, but the septa break and the placentae with the seeds are left in the middle of the ovary, as in *Oroxylum indicum* (Fam. Bignoniaceae, Fig. 149, A), thorn apple (*Datura metel*) of Fam. Solanaceae, *Pterospermum acerifolium* (Fam. Sterculiaceae), etc.



FIG. 149. DEHISCENCE OF CAPSULAR FRUITS (Diagrammatic)

A, septifragal ; B, septicidal ; C, loculicidal.

(d) *Porocidal*, when the opening takes place by means of pores at the apices of ripe carpels, as in opium poppy (*Papaver somniferum*) of Fam. Papaveraceae, toadflax (*Linaria ramosissima*) of Fam. Scrophulariaceae, etc.

(e) *Circumsessile* or *pyxis*, when dehiscence takes place along a circular horizontal line on the pericarp, and the upper lid, thus formed, is knocked off like the lid of a box exposing the seeds, as in *Amaranthus gangeticus*, cock's comb (*Celosia cristata*) and other plants of Fam. Amaranthaceae, *Portulaca oleracea* (Fam. Portulacaceae), members of Fam. Melastomaceae, etc.

C. SCHIZOCARPIC FRUITS OR SCHIZOCARPS (developed from a mono-, bi- or multi-carpellary gynaecium with an inferior or superior ovary, and splitting up at maturity into 1-seeded parts in such a manner that a portion of the pericarp always surrounds the seed).

The chief types of schizocarps (Fig. 150) are as follows :

Lomentum. It is a kind of pod with constriction between the seeds, and splits up transversely at the constrictions into 1-seeded pieces, as in *Acacia sphaerocephala* (Fig. 150, A), sensitive plant (*Mimosa pudica*) and other plants of S.F. Mimosae (Fam. Leguminosae), *Desmodium gyrans* and some other plants of S.F. Papilionaceae (Fam. Leguminosae).

Cremocarp. It is a 2-seeded fruit developed from a bicarpellary syncarpous gynaecium with an inferior ovary, and splits open from above downwards into 1-seeded indehiscent parts, called **mericarps**, which remain attached to the **carpophore**, as in coriander (*Coriandrum sativum*), anise (*Foeniculum vulgure*, Fig. 150, B & C) and other plants of Fam. Umbelliferae.

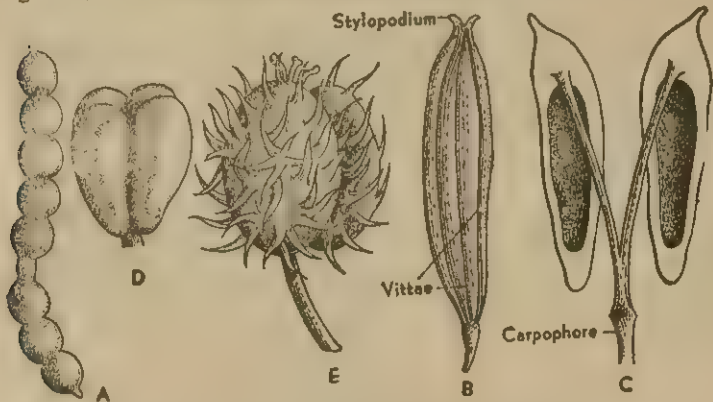


FIG. 150. SCHIZOCARPIC FRUITS

A, lomentum ; B-C, cremocarp ; D, carcerule ; E, regma.

Carcerule. It is developed from a bicarpellary syncarpous gynaecium with a superior, falsely 4-chambered ovary, and splits open into four 1-seeded indehiscent parts, as in basil (*Ocimum sanctum*, Fig. 150, D), sage (*Salvia plebeja*) and other plants of Fam. Labiatae, *Cynoglossum* and some other plants of Fam. Boraginaceae.

Regma. It is developed from a tri- or penta-carpellary syncarpous gynaecium with a superior, 3- or 5-chambered ovary, and splits open into three or five 1-seeded dehiscent parts, called **eoeci**, as in castor (*Ricinus communis*, Fig. 150, E) of Fam. Euphorbiaceae, *Geranium* sp. (Fam. Geraniaceae), etc.

II. FLESHY FRUITS

(Pericarp fleshy and indehiscent ; seeds are released only after the decay of the flesh tissue enclosing them.)

The following are the chief types of fleshy fruits (Fig. 151) :

Drupe or 'stone fruit'. It is usually a 1-seeded fruit, which is developed from a monocarpellary gynaecium with a superior ovary ; the pericarp is clearly differentiated into an outer exocarp, a middle fleshy mesocarp, and an inner hard endocarp forming the stone, as in mango (*Mangifera indica*, Fig. 151, A) of Fam. Anacardiaceae, peach (*Prunus persica*) and apricot (*Prunus armeniaca*) of Fam. Rosaceae, etc. In almond (*Prunus amygdalus*) of Fam. Rosaceae, the mesocarp is dry and tough, and sometimes contains two seeds.

In coconut (*Cocos nucifera*) of Fam. Palmae, the drupe is derived from a multicarpellary syncarpous gynaecium and the mesocarp is fibrous, hence, it is also known as **fibrous drupe**.

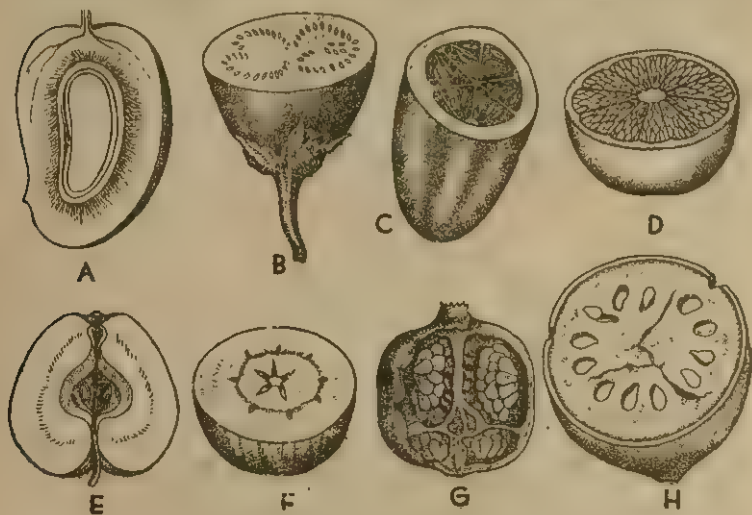


FIG. 151. FLESHY FRUITS (in sectional views)
A, drupe ; B, berry ; C, pepo ; D, hesperidium ; E-F, pome ; G, balausta ; H, amphisarca.

Pome. It is developed from a bi- or multi-carpellary gynaecium with an inferior ovary ; the outer skin and the thick flesh are derived from the cup-like wall of the receptacle, and the central

cartilaginous part (core) from the carpels, as in apple (*Pyrus malus*, Fig. 151, E & F) pear (*Pyrus communis*), quince (*Cydonia vulgaris*), etc., of Fam. Rosaceae, rose-apple (*Schyzium jambos*) of Fam. Myrtaceae is also a kind of pome, but the core is more or less papery.

Baccate fruits. All fleshy fruits, excepting drupe and pome, are known as *baccate* or *berry-like fruits*. The succulent mass is more or less pulpy and the seeds, which are usually hard, are embedded in the pulp. These fruits differ from drupe by the fact that the endocarp is never stony, but the three regions (exocarp, mesocarp and endocarp) may be differentiated.

The baccate fruits are of the following types :

(a) **Berry.** It is usually developed from a multicarpellary syncarpous gynaecium with a superior or inferior ovary having axile or parietal placentation ; the exocarp is usually thin, and the seeds lie free in the pulp. Brinjal (*Solanum melongena*, Fig. 151, B), tomato (*Lycopersicum esculentum*) and other plants of Fam. Solanaceae, papaw (*Carica papaya*) of Fam. Caricaceae, grape (*Vitis vinifera*) of Fam. Vitaceae, date (*Phoenix sylvestris*)* of Fam. Palmae, etc., are examples of superior berry ; while guava (*Psidium guayava*) of Fam. Myrtaceae, banana (*Musa paradisiaca* var. *sapientum*) of Fam. Musaceae, etc., are those of inferior berry.

(b) **Pepo.** It is developed from a tricarpellary syncarpous gynaecium with an inferior ovary having parietal placentation ; the exocarp is tough, and the seeds are attached to the placentae, as in cucumber (*Cucumis sativus*, Fig. 151, C), melon (*Cucumis melo*), gourd (*Cucurbita maxima*) and other plants of Fam. Cucurbitaceae.

(c) **Hesperidium.** It is a many-chambered fruit, which is developed from a multicarpellary gynaecium with a superior ovary having axile placentation, as in sweet orange (*Citrus sinensis*, Fig. 151, D), shaddock (*Citrus grandis*=*C. decumana*) and a few other plants of Fam. Rutaceae. The outer leathery rind is the mesocarp, the underlying white fibrous structure, the endocarp, and the inner membrane lining the loculi, the endocarp. The

*The date is usually regarded as a one-seeded berry with a thin, papery endocarp. But, it is also considered by some to be a type of drupe in which the endocarp, instead of becoming hard and stony, has become papery.

pulp consists of hairy outgrowths from the inner wall of the endocarp are filled up with a sweet juice.

(d) **Balausta.** It is a many-seeded, many-chambered fruit developed from an inferior ovary ; the pericarp is leathery and crowned by the persistent calyx-lobes. The yellow membranous structures found inside the fruit are the remnants of the carpels. The seeds are attached irregularly on the wall or at the centre. The edible portion is the succulent testa. Pomegranate (*Punica granatum*, Fig. 151, G) of Fam. Punicaceae is a familiar example.

(e) **Amphisarca.** It is a many-seeded, many-chambered fruit developed from a superior ovary ; the pericarp is somewhat woody, as in wood apple (*Aegle marmelos*, Fig. 151, H) and elephant apple (*Feronia limonia*=*F. elephantum*) of Fam. Rutaceae. The edible portion is developed from the placenta, while the mucilaginous substance around the seed is derived from the testa.

AGGREGATE FRUITS

It has already been stated that an aggregate fruit is a collection of small fruits developed from a single flower with apocarpous gynaecia. The collection of small fruits is known as an



FIG. 152. AGGREGATE FRUITS

A, etaerio of berris of *Artabotrys* ; B, etaerio of follicles of *Magnolia* ;

C, l.s. of a fruitlet of A ; D, hip of rose ; E, l.s. of the same ;

F, etaerio of achenes of *Clematis*.

etaerio. There may be etaerio of follicles, achenes, drupes and berries (Fig. 152).

Etaerio of follicles. The familiar examples are *Michelia champaca* and *Magnolia grandiflora* (Fig. 152, B) of Fam. Magnoliaceae, *Sterculia foetida* (Fam. Sterculiaceae), monk's hood (*Aconitum napellus*), larkspur (*Delphinium majus*) and some other plants of Fam. Ranunculaceae, *Calotropis procera* (Fam. Asclepiadaceae), *Alstonia scholaris*, periwinkle (*Vinca rosea*) and some other plants of Fam. Apocynaceae, etc.

Etaerio of achenes. Common examples are *Ranunculus sceleratus*, *Naravelia zeylanica*, *Clematis gouriana* (Fig. 152, F) and a few other plants of Fam. Ranunculaceae, lotus (*Nelumbo nucifera*=*Nelumbium speciosum*) of Fam. Nymphaeaceae, rose (*Rosa centifolia*) of Fam. Rosaceae, etc. It is to be noted that in lotus, the achenes are embedded in a fleshy top-shaped receptacle, while in rose, these are enclosed in a hollow jug-shaped one, and in the latter case, the entire structure is known as the 'hip' of roses.

Etaerio of drupes. The familiar examples are raspberry (*Rubus idaeus*), strawberry (*Fragaria vesca*), etc., of Fam. Rosaceae, where these are inserted on a fleshy receptacle.

Etaerio of berries. Common examples are *Artabotrys odoratissima* (Fig. 152, A & C) and *Polyalthia longifolia* of Fam. Anonaceae.

Custard apple (*Anona squamosa*, Fig. 153, A & B) and billock's heart (*Anona reticulata*) of Fam. Anonaceae are special aggregate fruits, since only one fruit is developed from a single



FIG. 153. SPECIAL AGGREGATE FRUIT
A, an entire fruit of custard apple ; B, l.s. of the same.

flower with apocarpous gynaecia. The apices of ripe carpels during development fuse together forming the rind of the fruit. *Dillenia indica* (Fam. Dilleniaceae) is also a special aggregate fruit consisting of many follicles enclosed within persistent and accrescent calyx.

MULTIPLE OR COMPOSITE FRUITS

The multiple or composite fruits (Fig. 154) are also known as *syncarps* or *infructescences*. These are of two kinds as discussed below.

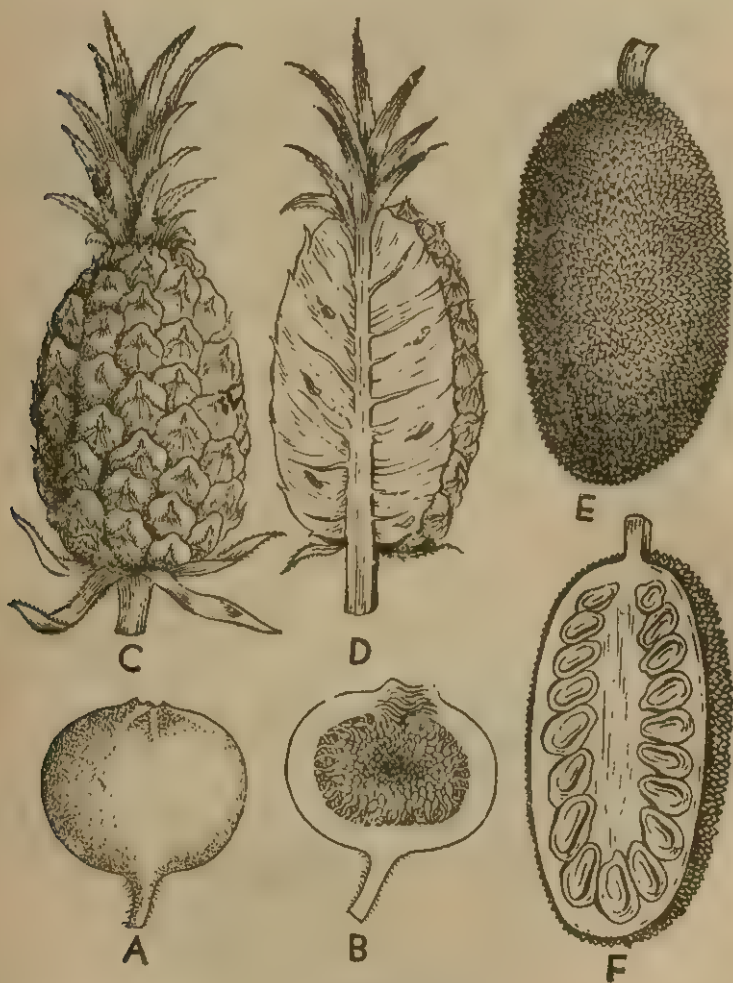


FIG. 154. MULTIPLE FRUITS

A-B, syconus of fig ; C-D, sorosis of pineapple ; E-F, sorosis of jackfruit.

Syconus. It is developed from the hypanthodium type of inflorescence with a hollow pear-shaped receptacle containing

many seeds. Banyan (*Ficus benghalensis*) and fig (*Ficus hispida*, *F. cunia*, Fig. 154, A & B), etc., of Fam. Moraceae are familiar examples.

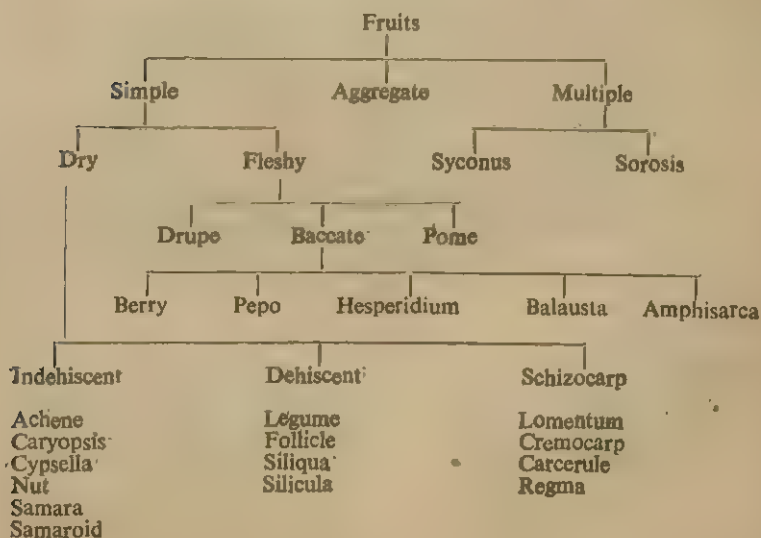
Sorosis. It is developed from a spicate pistillate inflorescence, in which the axis and the ovaries of the flowers are fused together forming a single fruit, as is found in pineapple (*Ananasa sativa*, Fig. 154, C & D) of Fam. Bromeliaceae, jackfruit (*Artocarpus integra*=*A. integrifolia*, Fig. 154, E & F) and mulberry (*Morus indica*) of Fam. Moraceae, etc.

In the pineapple, the outer portion of the rachis, perianths and bracts become fleshy, and all are fused together. The so-called hexagonal 'eye' on the surface represents a single flower. The seeds are rare, and the fruit bears at its apex a crown of foliage leaves.

In the jackfruit, the apical parts of the ripe carpels become fused forming a spiny rind. The rachis, lying inside the fruit, is club-shaped and woody, and bears many fleshy chambers in the axils of fleshy bracts. The outer fleshy covering of each chamber is enveloped by a membranous covering, which represents the testa.

In mulberry, the fleshy part is made up of the perianth.

Fruits may be tabulated as follows :



EDIBLE PARTS OF SOME COMMON FRUITS OF INDIA

| COMMON ENGLISH NAME | Name of fruit SCIENTIFIC NAME AND FAMILY | Type of fruit | Edible part |
|---------------------|--|--------------------------------|--|
| Apple | <i>Pyrus malus</i> (Rosaceae) | Pome | Fleshy thalamus |
| Banana | <i>Musa paradisiaca</i> var. <i>sapientum</i> (Musaceae) | Berry | Mesocarp + endocarp |
| Bean | <i>Phaseolus</i> sp. (Leguminosae) | Legume | Inner portion of pericarp Pericarp (of young fruits) as well as seeds |
| Black berry | <i>Eugenia jambolana</i> (Myrtaceae) | Berry | Pericarp + thalamus |
| Bottle gourd | <i>Lagenaria vulgaris</i> (Cucurbitaceae) | Pepo | Mesocarp + endocarp |
| Brinjal | <i>Solanum melongena</i> (Solanaceae) | Berry | Pericarp + placenta |
| Bullock's heart | <i>Anona reticulata</i> (Anonaceae) | Etacrio of berries (Aggregate) | Pericarp |
| Cape gooseberry | <i>Physalis peruviana</i> (Solanaceae) | Berry | Pericarp |
| Cashewnut | <i>Anacardium occidentale</i> (Anacardiaceae) | Nut | Cotyledons as well as the fleshy axis |
| Coconut | <i>Cocos nucifera</i> (Palmae) | Fibrous drupe | Endosperm and cotyledon |
| Cucumber | <i>Cucumis sativus</i> (Cucurbitaceae) | Pepo | Mesocarp + endocarp |
| Custard apple | <i>Anona squamosa</i> (Anonaceae) | Etacrio of berries (Aggregate) | Pericarp |
| Date | <i>Phoenix sylvestris</i> (Palmae) | Berry (or drupe) | Mesocarp |
| Elephant apple | <i>Feronia limonia</i> = <i>F. elephantum</i> (Rutaceae) | Amphisarca | Succulent placenta + inner portion of pericarp |
| Fig | <i>Ficus</i> sp. (Moraceae) | Syconus | Receptacle |
| Grape | <i>Vitis vinifera</i> (Vitaceae) | Berry | Pericarp + placenta |
| Groundnut | <i>Arachis hypogaea</i> (Leguminosae) | Legume | Cotyledons |
| Guava | <i>Psidium guayava</i> (Myrtaceae) | Berry | Pericarp + thalamus |
| Jackfruit | <i>Artocarpus integrifolia</i> (Moraceae) | Sorosis | Bract, perianth and seed |
| Lady's finger | <i>Hibiscus esculentus</i> (Malvaceae) | Capsule | Entire young fruit |

| COMMON ENGLISH NAME | SCIENTIFIC NAME AND FAMILY | Name of fruit | Type of fruit | Edible part |
|---------------------|--|---------------|---------------|--|
| Lemon | <i>Citrus limon</i> (Rutaceae) | | Hesperidium | Juicy unicellular hairy outgrowths from the inner wall of the endocarp |
| Litchi | <i>Litchi chinensis</i> (Sapindaceae) | | Nut } | Fleshy aril |
| Longan | <i>N. longana</i> (Sapindaceae) | | Nut } | Endosperm + embryo |
| Maize | <i>Zea mays</i> (Gramineae) | | Caryopsis | Mesocarp |
| Mango | <i>Mangifera indica</i> (Anacardiaceae) | | Drupe | Fleshy aril |
| Mangosteen | <i>Garcinia mangostana</i> (Guttiferae) | | Berry | Mesocarp + endocarp as well as a portion of the receptacle |
| Melon | <i>Cucumis melo</i> (Cucurbitaceae) | | Pepo | As in lemon |
| Orange | <i>Citrus sinensis</i> (Rutaceae) | | Hesperidium | Mesocarpic juice as well as cotyledon and endosperm |
| Palmyra palm | <i>Borassus flabellifer</i> (Palmae) | | Drupe | Mainly cotyledons |
| Pea | <i>Pisum sativum</i> (Leguminosae) | | Legume | Epicarp + mesocarp |
| Peach | <i>Prunus persica</i> (Rosaceae) | | Drupe | Fleshy thalamus |
| Pear | <i>Pyrus communis</i> (Rosaceae) | | Pome | Fused fleshy rachis, bract, perianth and pericarp |
| Pineapple | <i>Ananas sativus</i> (Bromeliaceae) | | Sorosis | Epicarp + mesocarp |
| Plum | <i>Prunus domestica</i> (Rosaceae) | | Drupe | Succulent testa |
| Pomegranate | <i>Punica granatum</i> (Punicaceae) | | Balausta | Mainly endosperm |
| Rice | <i>Oryza sativa</i> (Gramineae) | | Caryopsis | Fused pericarp and thalamus |
| Roseapple | <i>Eugenia jambos</i> (Myrtaceae) | | Berry | As in lemon |
| Shaddock | <i>Citrus grandis</i> = <i>C. decumana</i> (Rutaceae) | | Hesperidium | As in cucumber, as well as seeds |
| Sweet gourd | <i>Cucurbita maxima</i> (Cucurbitaceae) | | Pepo | Mesocarp + endocarp |
| Tamarind | <i>Tamarindus indica</i> (Leguminosae) | | Lomentum | Pericarp + placenta |
| Tomato | <i>Lycopersicum esculentum</i> (Solanaceae) | | Berry | Cotyledons |
| Walnut | <i>Juglans regia</i> (Juglandaceae) | | Drupe | Endosperm + embryo |
| Wheat | <i>Triticum aestivum</i> = <i>T. vulgare</i> (Gramineae) | | Caryopsis | As in elephant apple |
| Wood apple | <i>Aegle marmelos</i> (Rutaceae) | | Amphisarca | |

ECONOMIC IMPORTANCE OF FRUITS

The majority of the common fruits are usually taken in a raw state. These form very valuable diets and are important sources of vitamins, as in apple, pear, orange, lemon, grape, mango, banana, papaw, pineapple, etc. Quite a good number of fruits are used in cooked or pickled form, such as squash, gourd, cucumber, tomato, chilli, etc. A kind of flour is obtained from the bread fruits (*Artocarpus incisa*) of Fam. Moraceae. The fruits of olive (*Olea europea*) of Fam. Oleaceae is the source of the widely used olive oil. The dried fruit of vegetable sponge (*Luffa aegyptiaca*) of Fam. Cucurbitaceae is used as a bath sponge or an oil-filter ; it also yields an important kind of fibre. From the fibrous mesocarp of coconut mattresses and ropes are prepared. The latex of unripe fruits of opium poppy (*Papaver somniferum*) of Fam. Papaveraceae yields the powerful narcotic opium, used by the physicians as a sedative in the forms of morphine and codeine. The latex of the unripe fruits of papaw (*Carica papaya*) of Fam. Caricaceae possesses a digestive property, due to the presence of the enzyme papain, and is often used to make meat tender in cooking. The viscid mucous of the fruits of *Diospyros embryopteris* (Fam. Ebenaceae) is used for making the bottoms of boats as well as fishing nets water-tight. The juice of the fruit of marking nut (*Semecarpus anacardium*) of Fam. Anacardiaceae is used by the washermen for marking clothes. The fruit of *Vanilla*, an orchid, furnishes the vanilla of commerce, used in the preparation of cold drinks and chocolates.

CHAPTER X

DISPERSAL OF FRUITS AND SEEDS

If the fruits or the seeds, after being set free, be deposited on the soil directly under the parent plant, these cannot find all the conditions favourable for germination. The light and the air may not be quite adequate for them ; the soil also cannot supply them with requisite amount of food materials, since these have been already mostly used up by the parent plant. Consequently, the seedlings become weak and degenerated. Further, there takes place a struggle for existence amongst themselves, and most of them are liable to perish under such unfavourable conditions. Thus, in order to enable the seeds to maintain the race, wonderful provisions have been made by nature to scatter them to localities far away from the parent plant, so that they may find the conditions favourable for their growth.

Plants have no power of locomotion, nor have the power of throwing their fruits and seeds to a great distance. Hence, they are to depend on some agents for their dispersal. The chief agents are wind, water and animals (including birds). Sometimes the fruits are provided with explosive mechanisms to serve this purpose.

I. DISPERSAL BY WIND

The essential condition for dispersal by wind is the lightness of fruits or seeds in proportion to their bulk, or a floating device, which increases their surface without greatly increasing the weight. Plants, which require the agency of wind for the dispersal of their fruits or seeds, are known as **anemochorous** ones.

The seeds of orchids (Fam. Orchidaceae) are very small and light, so they can be easily carried away by the wind.

Censer mechanism. When the dehiscent fruits, like capsules and follicles, dehisce partially at the apex or by means of pores or teeth, seeds come out of them, a few at a time, when shaken

by the wind. The familiar examples are opium poppy (*Papaver somniferum*) and Mexican poppy (*Argemone mexicana*) of Fam. Papaveraceae, monk's hood (*Aconitum napellus*) of Fam. Ranunculaceae, *Aristolochia gigans* (Fam. Aristolochiaceae), etc.

Parachute mechanism. The fruits and seeds, which are provided with hairy or winged outgrowths (Fig. 155) acting as parachutes, are readily carried away by the wind.

(a) *Hairy outgrowths.* The seeds of cotton (*Gossypium herbaceum*) of Fam. Malvaceae are provided with hairs all over

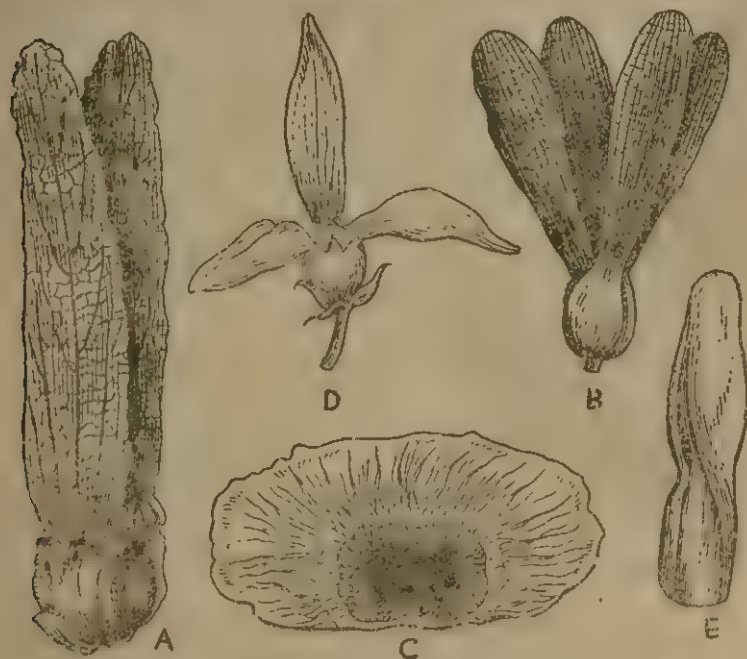


FIG. 155. FRUITS AND SEEDS WITH OUTGROWTHS

A, samaroid fruit of *Dipterocarpus* with wings; B, samaroid fruit of *Shorea* with wings; C, winged seed of *Oroxylum*; D, samara of *Hiptage*; E, winged seed of mahogany.

their bodies. The seeds of oleander (*Nerium peruvianum*=*N. odorum*) of Fam. Apocynaceae are provided with hairs at both ends, while those of *Calotropis procera* (Fam. Asclepiadaceae) are provided with hairs at one end only. The fruits of *Blumea lacera*, *Vernonia cinerea* and many other plants of Fam. Com-

positae are provided with the **pappus**. The fruits of *Naravelia zeylanica* and *Clematis gouriana* of Fam. Ranunculaceae are provided with persistent hairy styles, while those of *Andropogon sorghum* (Fam. Gramineae) have abundant silky hairs.

(b) *Winged outgrowths*. The seeds of horse radish (*Moringa pterygosperma*) of Fam. Moringaceae, *Sterculia foetida*, *Pterospermum acerifolium* and many other plants of Fam. Sterculiaceae, *Oroxylum indicum* (Fig. 155, C), *Stereospermum chelonoides*, *S. suaveolens* and many other plants of Fam. Bignoniaceae, *Cedrela toona*, Indian satin-wood (*Chloroxylon swietenia*), and mahogany (*Swietenia mahagoni*, Fig. 155, E) of Fam. Meliaceae, etc., have testas flattened into wings. (2) The fruits of *Hiptage madablota* (Fam. Malpighiaceae, Fig. 155, D), country almond (*Terminalia catappa*), and *T. arjuna* of Fam. Combretaceae, *Dioscorea alata* (Fam. Dioscoreaceae), etc., have their pericarps expanded into wings, while those of *Shorea robusta* (Fig. 155, B) *Dipterocarpus* sp. (Fig. 155, A) and many other plants of Fam. Dipterocarpaceae are provided with persistent sepals, which act as wings.

II. DISPERSAL BY WATER

The dispersal by water is less common, and is met with in some water plants and plants growing on the river banks or seashores. Those fruits and seeds, which are dispersed by water, have floating devices and water-tight coverings. The plants, requiring the agency of water for such dispersals, are known as **hydrochorous** ones.

The fruits of coconut (*Cocos nucifera*), betel nut (*Areca catechu*), *Nipa fruticans* and other plants of Fam. Palmae have watertight coverings and abundant air spaces, so that they can easily float on water and be drifted away by its current.

The fruitlets of lotus (*Nelumbo nucifera* = *Nelumbium speciosum*) of Fam. Nymphaeaceae lie embedded in the spongy and watertight thalamus, and thus can be carried by the current of water.

The seeds of many aquatic plants, such as water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae, *Alisma plantago*, *Butomopsis lanceolatus*, *Sagittaria sagittifolia* and other plants of Fam. Alismataceae, etc., have air spaces in their coverings, which

enable them to float on water, so that they can be carried away easily by its current.

III. DISPERSAL BY ANIMALS

Those fruits and seeds, which are dispersed by animals, are either provided with adhering apparatus, or they are fleshy in nature. Plants possessing such devices are known as **zoochorous** ones.

Many dry fruits or seeds possess spines, hooks, barbs, bars or sticky glands, which cause them to adhere to the bodies of the grazing or passing animals, or to the clothings of men, who happen to brush against them, and are thus transported to a great distance. The fruits of *Andropogon aciculatus* (Fam. Gramineae), *Achyranthes aspera* (Fam. Amaranthaceae), etc., are provided with spines, while those of *Urena lobata* (Fam. Malvaceae), spiny cocklebur (*Xanthium strumarium*) of Fam. Compositae, *Triumfetta rhomboidea* (Fam. Tiliaceae), and *Martynia diandra* (Fam. Martyniaceae), etc., are provided with hooked bars. Sticky glands are present on the fruits of *Boerhaavia repens* (Fam. Nyctaginaceae), *Polanisia icosandra* (= *Cleome viscosa*) of Fam. Capparidaceae, etc., as well as on the calyx of *Plumbago* sp. (Fam. Plumbaginaceae).

The fleshy fruits possess beautiful colour or taste, or both, and thus they invite the attraction of animals, particularly, the birds. Crows and other birds are attracted from a long distance by the red colour of the fruits of banyan (*Ficus benghalensis*) of Fam. Moraceae, and while feeding upon them, scatter a few seeds in the process. This accounts for the presence of such plants on the roofs and cornices of old buildings, temples, and tree-tops. The dehiscent pods of *Abrus precatorius* of S.F. Papilionaceae (Fam. Leguminosae) are taken by birds as caterpillars, but subsequently, when the mistake is detected, they are thrown away, and thus the seeds are dispersed. In many cases, as in mango (*Mangifera indica*) of Fam. Anacardiaceae, litchi (*Litchi chinensis* = *Nephelium litchi*) of Fam. Sapindaceae, etc., birds and animals devour the sweet pulp and reject the stones, thus dispersing the seeds ; if these fall on suitable soils, new plants ultimately spring up. Similarly, bats and squirrels distribute the nuts of ground nut (*Arachis hypogea*) of S.F. Papilionaceae (Fam.

Leguminosae), betel nut (*Areca catechu*) of Fam. Palmae, etc. The jackals and bears are very fond of date (*Phoenix sylvestris*) of Fam. Palmae, jujube (*Zizyphus jujuba*) of Fam. Rhamnaceae, etc., and when they devour the fruits, the seeds, which are protected by hard coverings or testa, are not acted upon by the digestive juice of the stomach. Afterwards, they pass out of the animal body with the excreta uninjured, and wherever the droppings fall, new plants spring up. Many aquatic birds, such as ducks, snipes, etc., carry the sticky or small fruits and seeds on their feet, and while they go from one pond to another in quest of food, the fruits and seeds are scattered.

IV. DISPERSAL BY EXPLOSIVE MECHANISM

In some cases, when the fruits rupture, the seeds are thrown elastically out of them. This method has only a limited effect, as the seeds are distributed for a short distance only. The explosive mechanism is found in the following cases. The ripe fruits of balsam (*Impatiens balsamina*) of Fam. Balsaminaceae, and wood sorrel (*Oxalis corniculata*) of Fam. Oxalidaceae burst suddenly when touched; the valves twist upwards, and the seeds shoot out in all directions. The ripe fruits of *Ruellia tuberosa*, *Barleria prionitis* and many other plants of Fam. Acanthaceae, when come in contact with moisture, burst suddenly with an explosive sound, and the seeds are scattered; sometimes, the seeds are provided with **jaculators** (curved hooks), which straighten out and help in their dispersal. The legumes of pea (*Pisum sativum*), *Clitoria ternatea* and many other plants of S.F. Papilionaceae (Fam. Leguminosae), capsules of *Helicteres isora* (Fam. Sterculiaceae), etc., when mature, burst into valves, which subsequently twist upwards, and thus the seeds are ejected with some force. The fruit of castor (*Ricinus communis*) of Fam. Euphorbiaceae usually breaks up elastically, and thus the seeds are dispersed. The fruits of vegetable sponge (*Luffa aegyptiaca*) of Fam. Cucurbitaceae discharge their seeds with great force through the holes left at one end, when these drop off from their stalks. A similar mechanism of seed dispersal is also noted in the 'squirt-ing cucumber' (*Ecballium elaterium*), a cucurbitaceous plant of the Mediterranean region.

CHAPTER XI

THE SEED AND ITS GERMINATION

The seed is a fertilized and fully ripened megasporangium (ovule) enclosed within one or two layers of integuments (seed coats) and containing within it an embryo or a rudimentary plant in the dormant state.

Seeds may be differentiated into several types, according to the number of cotyledons, or, according to the storage of food materials in them.

Depending on the number of cotyledons, seeds as well as the plants bearing them may be : (1) **monocotyledonous**, *i.e.*, with one cotyledon only, as in cereals, grasses and other plants belonging to Fam. Gramineae, palm (Fam. Palmae), orchids (Fam. Orchidaceae), *etc.*, (2) **dicotyledonous**, *i.e.*, with two cotyledons, as in pulses of S.F. Papilionaceae (Fam. Leguminosae), tamarind (*Tamarindus indicus*) of S.F. Caesalpinieae (Fam. Leguminosae), mango (*Mangifera indica*) of Fam. Anacardiaceae, sunflower (*Helianthus annuus*) of Fam. Compositae, *etc.* ; and (3) **polycotyledonous**, *i.e.*, with more than two cotyledons, as in pine (a gymnosperm).

According to the storage of food materials*, seeds may be : (1) **exalbuminous** or **non-endospermic**, where the food is stored up inside the cotyledon (*e.g.*, *Amorphophallus* of Fam. Araceae, *Alisma* of Fam. Alismataceae, *Vallisneria* of Fam. Hydrocharitaceae, *etc.*) or cotyledons, as in pea (*Pisum sativum*), gram (*Cicer arietinum*) and other plants of S.F. Papilionaceae (Fam. Leguminosae), tamarind, mango, sunflower, *etc.*, and (2) **albuminous** or **endospermic**, where the food is stored up outside the cotyledon or cotyledons in a separate tissue known as the **endosperm**, as in paddy (*Oryza sativa*), wheat (*Triticum aestivum* = *T. vulgare*), maize (*Zea mays*) and other plants of Fam. Gramineae, castor (*Ricinus communis*) of Fam. Euphorbiaceae, custard apple (*Anona squamosa*) of Fam. Anonaceae, *etc.*, as well as in another tissue,

*The principal kinds of stored food materials are (a) *carbohydrates*, mainly starch, hemicellulose and sugars, (b) *fats and oils*, and (c) *proteins*.

called the **perisperm**, as in water lily (*Nymphaea stellata*) and other plants of Fam. Nymphaeaceae, black pepper (*Piper nigrum*) and other plants of Fam. Piperaceae, banana (*Musa paradisiaca* var. *sapientum*), Indian shot (*Canna indica*) and other plants belonging to the Order Scitamineae.

Seeds may be of various forms and sizes, varying from the dusty seeds of some orchids to huge seeds of the double coconut (*Lodoicea maldivicum*=*L. sechellarum*) of Fam. Palmae. They may be rounded, oval, ovoid, obovoid, elliptical, reniform, elongated, disc-shaped or extremely irregular.

GENERAL STRUCTURE OF SEEDS

A mature seed consists of two parts : one or two seed coats and a kernel.

SEED COATS. The seed coats are developed from the integuments of the ovule. They are usually two in number, the outer one is known as the **testa**, and the inner one, the **tegmen**.

The tegmen is very delicate and usually much thinner than the testa ; it may remain free from the testa, as in gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, or closely adpressed to it, as in gram (*Cicer arietinum*) of S.F. Papilionaceae (Fam. Leguminosae). Sometimes, the tegmen is absent, as in pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae).

The testa is usually *tough and leathery*, as in pea (*Pisum sativum*), gram (*Cicer arietinum*) and other plants of S.F. Papilionaceae (Fam. Leguminosae), or *hard and horny*, as in castor (*Ricinus communis*) of Fam. Euphorbiaceae ; it may also become *soft, succulent and fleshy*, as in pomegranate (*Punica granatum*) of Fam. Punicaceae, *coriaceous*, as in gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae. The testa is generally *brownish* in colour, but also may be *whitish* or *yellowish*, as in pea, poppy (*Papaver somniferum*) of Fam. Papaveraceae, *black*, as in Indian shot (*Canna indica*) of Fam. Cannaceae, *red*, as in crab's eye (*Abrus precatorius*) of S.F. Papilionaceae (Fam. Leguminosae), *mottled*, as in castor, and of various appearances ; it may be perfectly *smooth*, as in pea, or *wrinkled*, as in cumin seed (*Nigella sativa*, Fig. 156, C) of Fam. Ranunculaceae, *ridged and furrowed*, as in larkspur (*Delphinium majus*, Fig. 156, B) of Fam. Ranunculaceae, *pitted*, as in poppy, *striated*, as in tobacco (*Nico-*

tiana tabacum) of Fam. Solanaceae, *reticulate* as in water cress (*Nasturtium officinale*, Fig. 156, A). of Fam. Cruciferae, or *spiny*, as in mulberry (*Morus indica*) of Fam. Moraceae. The testa is often provided with different kinds of appendage for

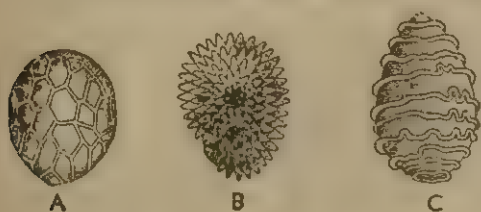


FIG. 156. NATURE OF TESTA

A, reticulate ; B, ridged and furrowed ;
C, wrinkled.

effective dispersal of seeds. Somewhere on the testa there is a scar, called the **hilum**, which indicates the position where the seed was attached to its stalk, the **funiculus**. Near about the hilum

there is a minute opening, called the **micropyle**, through which usually water oozes out, when a soaked seed is gently pressed. Sometimes, a ridge, called the **raphe**, is found on the testa caused by the bending of the seed against the funiculus, as in bean (*Vigna catjang*) of S.F. Papilionaceae (Fam. Leguminosae).

Besides the testa and the tegmen, there are occasionally found on the surface of some seeds an additional coat or integument, called the **arillus** or **aril**, as in litchi (*Litchi chinensis*—*Nephelium litchi*), longan (*Nephelium longana*) and other plants belonging to Fam. Sapindaceae, water lily (*Nymphaea stellata*) of Fam. Nymphaeaceae, *Baccauria sapida* (Fam. Euphorbiaceae), etc., which is developed from the apex of the funiculus ; sometimes, it is produced from both the hilum and the micropyle, as in nutmeg (*Myristica fragrans*) of Fam. Myristicaceae, and is then known as the **arillode** or **false aril**. In some cases, there are small irregular protuberances, developed on various parts of the seed, known as the **caruncles**, as in castor, and **strophioles**, as in gram.*

KERNEL. On removing the seed coats, the kernel is exposed. The kernel may either consist of the embryo only, as in all exalbuminous seeds, or of the embryo enclosed within the

*There is a great diversity of opinion as regards the morphological nature of these structures. According to some botanists, these two terms are synonymous, while others regard them as distinctly separate structures. The latter group holds that the caruncle is a micropylar development, as in castor (*Ricinus communis*) of Fam. Euphorbiaceae, and the strophiole is a funicular outgrowth, as in gram (*Cicer arietinum*), lablab (*Dolichos, lablab*) and other plants of S.F. Papilionaceae (Fam. Leguminosae).

endosperm, as in all albuminous seeds, or of the embryo along with both endosperm and perisperm, as in cardamom (*Elettaria cardamomum*) of Fam. Zingiberaceae, water lily, etc.

EMBRYO. The embryo is the baby plant enclosed within the seed. It usually consists of an axis (**tigellum**) and one or two **cotyledons**.

The cotyledons, though morphologically leaves, are usually highly modified in form, shape, colour and texture, and do not resemble the ordinary foliage leaves. They may be perfectly straight or somewhat folded or even rolled up. In the exalbuminous seeds, they are very thick and fleshy, since food matters are stored up within their body, while in albuminous seeds, they are very thin, delicate and leafy, since food matters are stored up outside their body. Besides acting as organs of food-storage, the cotyledons are also absorbing organs, and in some cases, as in gourd (*Cucurbita maxima*) of Fam. Cucurbitaceae, castor (*Ricinus communis*) of Fam. Euphorbiaceae, etc., after germination of seeds, they act as true functioning leaves helping in assimilation. They also protect the first terminal bud of the embryo (**plumule**). In monocotyledonous seeds, specially in the grass family, a special structure, called the **scutellum**, is usually regarded as the single cotyledon. In some palms, such as palmyra palm (*Borassus flabellifer*), date palm (*Phoenix sylvestris*), etc., belonging to Fam. Palmae, the cotyledon helps the plumule and the radicle to come out of the seed coat, while in others, it acts as a sucker for absorption of endosperm, e.g., coconut (*Cocos nucifera*) as well as palmyra palm of Fam. Palmae.

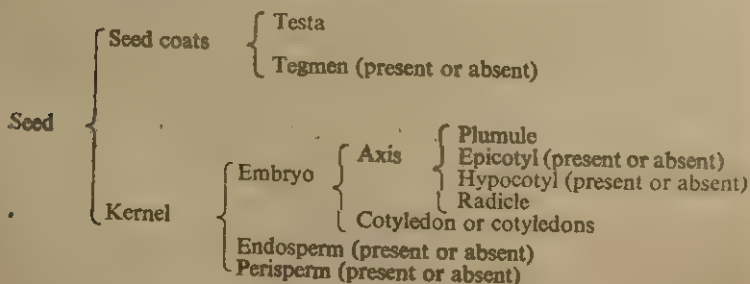
In dicotyledonous seeds, the two cotyledons are attached laterally at some point (**nodal zone**) on the axis of the embryo. The portion of the axis above the point of attachment of the cotyledons is known as the **epicotyl**, while that below the point of attachment is the **hypocotyl**. The growing tip of the epicotyl is called the **plumule**, and that of the hypocotyl is generally known as the **radicle**. In some cases, the epicotyl and the hypocotyl are extremely short and compressed, as in castor ; in others, they are totally absent, as in monocots. The plumule is the first terminal bud of the embryo and may consist only of a mass of undifferentiated tissue or of partially differentiated leaves, and finally develops into the first vegetative shoot. The radicle usually remains

as a mass of undifferentiated tissue, and subsequently gives rise to the first root of the plant. In monocotyledonous seeds, both the plumule and the radicle remain covered by protective sheaths, known as **coleoptile** and **coleorhiza** respectively. It may be noted that in all dicotyledonous seeds, the plumule is the terminal member and cotyledons are lateral members, while in all monocotyledonous ones, the plumule is the lateral member and the cotyledon is the terminal one.

ENDOSPERM. The endosperm is a kind of tissue which acts as the food-reservoir in albuminous seeds. It may be (i) *farinaceous* or *mealy* or *starchy*, as in wheat (*Triticum aestivum* = *T. vulgare*), maize (*Zea mays*) and other cereals of Fam. Gramineae; (ii) *oily*, as in mustard (*Brassica nigra*) of Fam. Cruciferae, Mexican poppy (*Argemone mexicana*) of Fam. Papaveraceae, castor (*Ricinus communis*) of Fam. Euphorbiaceae, etc.; (iii) *proteinaceous*, as in pulses; (iv) *corneous* or *horny*, as in coffee (*Coffea arabica*) of Fam. Rubiaceae, date (*Phoenix sylvestris*) of Fam. Palmae, etc.; (v) *fleshy*, as in *Amaryllis* (Fam. Amaryllidaceae), barberry (*Berberis vulgaris*) of Fam. Berberidaceae, etc.; (vi) *mucilagenous*, as in mallow (*Malva* sp.) of Fam. Malvaceae; (vii) *cartilagenous*, as in some members of Fam. Liliaceae; (viii) *ruminated* (i.e., marked by transverse lines of divisions, thus giving a marbled appearance), as in custard apple (*Anona squamosa*) and other plants of Fam. Anonaceae, betel nut palm (*Areca catechu*) of Fam. Palmae, etc.

PERISPERM. The perisperm is the remnant of the nucellus of the ovule. Like endosperm, it is also nutritive in function. Among the monocots, copious perisperm is present in the order Scitamineae.

The general structure of seeds may be tabulated as follows :



STRUCTURE OF A FEW COMMON SEEDS

A. DICOTYLEDONOUS SEEDS

Pea seed (*Pisum sativum*, Fig. 157).

The seed is exalbuminous. It is more or less rounded in shape, and is covered by a semi-transparent and leathery testa. On the testa there is a scar, the hilum, and near about it lies the micropyle. On removing the testa, the kernel or the embryo is

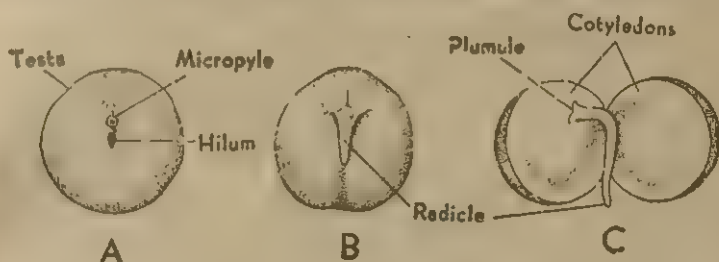


FIG. 157. STRUCTURE OF A PEA SEED

A, an entire seed ; B, the same with testa removed ; C, embryo split open.

exposed. It consists of two thick and fleshy cotyledons, hinged laterally on the axis of the embryo showing plumule and radicle.

Gram seed (*Cicer arietinum*, Fig. 158).

Like pea, it is also an exalbuminous seed. Each seed is more or less rounded, but pointed at one end. At one side it is slightly

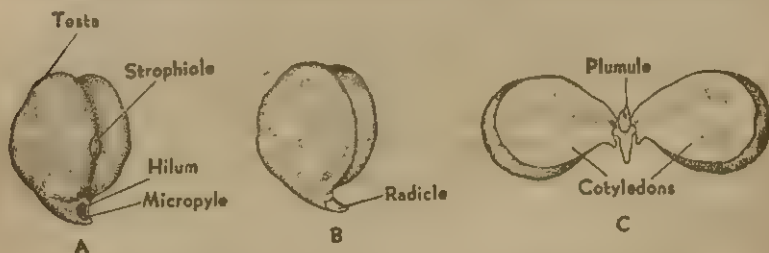


FIG. 158. STRUCTURE OF A GRAM SEED

A, an entire seed ; B, the same with testa and tegmen removed ; C, embryo.

convex, and, on the other, somewhat flattened. As usual, it is surrounded externally by a brown, thick and resistive testa, to

the inner side of which the tegmen is closely adpressed. The micropyle and the hilum are present on the testa, and lie very close together towards the pointed end of the seed. The strophiole also is present on the testa as a somewhat swollen ridge near about the middle of the flat side. On removing the seed coats, the kernel or the embryo is exposed. The embryo, as usual, consists of an axis and two fleshy cotyledons.

Castor seed (*Ricinus communis*, Fig. 159).

The seed is albuminous and is more or less oblong in shape. It is covered by a hard shell-like and brittle testa with peculiar

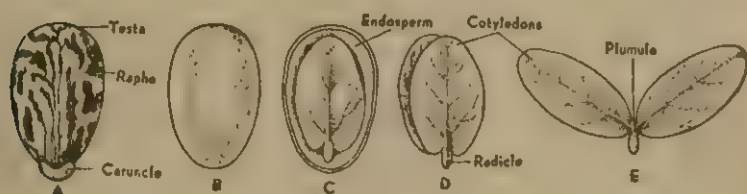


FIG. 159. STRUCTURE OF A CASTOR SEED

A, an entire seed ; B, the same with testa removed ; C, kernel cut lengthwise ; D, embryo ; E, embryo split open.

markings on its dark polished surface. Towards its narrow end there is a small spongy structure (*caruncle*), completely covering the micropyle. It absorbs water at the time of germination. Almost obscured by the caruncle and lying near the micropyle is the hilum. A raphe, running almost about the entire length of the seed, is also present on the testa. On cracking open and removing the testa, a slightly flattened, whitish, oval mass is visible, still remaining covered by a white, thin, papery structure.* The kernel is exposed on removing this layer, which is adpressed to it. The kernel, in this case, consists of the embryo and an oily endosperm, which can be clearly seen by cutting it (the kernel) lengthwise. The embryo consists of two thin, leaf-

*According to some botanists, this structure is the remnant of the perisperm, while others consider it as the tegmen or as the inner layer of the testa.

like cotyledons showing veins, and these are laterally attached to the sides of a very short axis showing the plumule, a very short hypocotyl and the radicle. The impressions of the veins of the leafy cotyledons can be clearly seen on the endosperm lying in contact with them.

B. MONOCOTYLEDONOUS SEEDS

Maize or Indian corn (*Zea, mays* Fig. 160).

The maize grains are really fruits, each containing a tightly-fitting seed inside. The grains, when examined *in situ*, i.e., when still attached to the axis of the cob, will be found to be incompletely surrounded at the base by four white and membranous structures, called

glumes and paleae. Externally, each grain is more or less flattened and oblong in shape. On one side of it, there is an opaque, whitish **deltoid area**, which indicates the position of the embryo inside

the common semi-transparent wall. The common wall is made up of the fruit wall (**pericarp**) and the seed coat inseparably fused together. The slight stalk-like structure present at the base of the grain represents the persistent pedicel of the fruit, and not the funiculus. When this coating is removed, the kernel is exposed, which is usually concave on the side of the embryo. The main bulk of the kernel is the endosperm, at one side of which the embryo is situated. The outermost layer of the endosperm, lying in contact with the common wall, is known as the **aleurone layer**. The remaining part of the endosperm is very frequently differentiated into an outer horny endosperm and an inner starchy endosperm, the former containing more protein substance than the latter. The embryo consists of one cotyledon (**scutellum**, the outermost layer of which is known as the **epithelial layer**) and an axis showing the plumule covered by the coleoptile, and the radicle covered by the

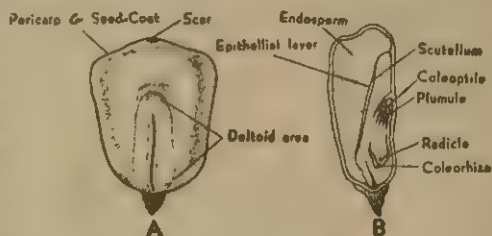


FIG. 160. STRUCTURE OF A MAIZE GRAIN
A, an entire grain ; B, the same cut lengthwise.

coleorrhiza respectively.* It is to be noted that there is a conical structure opposite the scutellum, which is known as the epiblast, and is regarded by some as the second suppressed cotyledon.

Paddy or unhusked rice (*Oryza sativa*, Fig. 161).

Like wheat grains, each paddy is a fruit having a seed inside. The fruit is externally surrounded by three alternating glumes and a palea. The first two, called **empty glumes**, are very small, white, scale-like and are placed outermost, occupying the base of the fruit. The third

glume, the **flowering glume**, or **lemma** (sometimes called the **inferior palea**) is the largest, yellow and scaly. In some varieties, the lemma bears

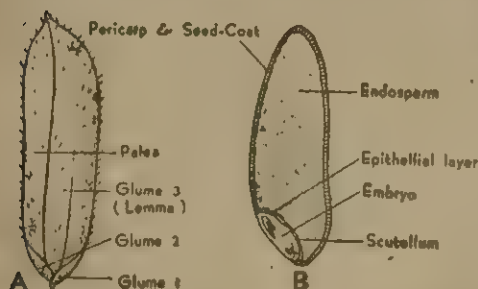


FIG. 161. STRUCTURE OF A PADDY GRAIN

A, an entire grain ; B, the same cut lengthwise.

awns, which may be either terminal or dorsal in position. These awns are highly hygroscopic, and help in the dispersal of fruit and also in attaching it to the soil during germination. The three glumes collectively constitute the **husk**. The third glume partially envelops the fruit and alternates with the **palea**, which is the fourth or innermost scaly structure overlapping the rest of the fruit. On removing the glumes and the palea, the grain is exposed. Within the common wall (usually reddish-brown in colour), as is usual in such cases, there is the kernel consisting of a massive endosperm, at one corner of which lies a minute embryo. The structure of the embryo is more or less like that of the maize grain. It is to be noted that the epiblast

*If a soaked grain is cut vertically through the embryo and the endosperm and a drop of iodine added to the cut surface, it becomes distinguished into two areas : (1) the main bulk, which turns black, is the endosperm, and (2) a less dense, lighter area, which does not change in colour, is the embryo.

in this case is a rim-like structure in continuation with the scutellum.

Paddy=a mature spikelet of the rice plant
 =glumes 1, 2, 3+palea+grain
 =husk+palea+grain

The interpretations as regards the real morphological nature of the scutellum, the epiblast and the germ-sheath, as discussed by A. B. Rendle*, are as follows :—

I. MIRBEL (1810)

1. Scutellum=cotyledon ;
2. epiblast = a rudimentary second cotyledon ;
3. sheath = an expanded part of the cotyledon comparable with that which occurs in most monocotyledons.

In 1815, however, he calls the sheath a **pileole** or primordial leaf, assuming therefore that the three organs represent three distinct leaves.

II. RICHARD (1811)

1. scutellum = an absorptive organ ;
2. epiblast = a prolongation of the scutellum ;
3. sheath = the single cotyledon, which, as in other monocotyledons, envelops the plumule.

III. SCHLEIDEN (1864)

1. Scutellum = the single cotyledon ;
2. epiblast = a part of the sheath of the cotyledon ;
3. sheath = the primordial leaf succeeding the cotyledon.

IV. SACHS (1868)

1. scutellum = an absorptive organ developed on the internode below the cotyledon and comparable functionally, but not morphologically, with the sucker-like tip of the cotyledon of palms and other monocotyledons ;

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2. sheath = the single cotyledon.

Thus, the three structures may represent three or two leaves or a single leaf.

V. VAN TIEGHEM (1872)

1. scutellum = cotyledon ;
2. epiblast = a cellular outgrowth of the sheath of the cotyledon ;
3. sheath = a united pair of stipules (bistipular sheath) of the cotyledon.

On the whole, the view holds that scutellum and pileole (or germ-sheath) represent highly differentiated parts of a single cotyledon.

Besides these, there are two other views as follows :

VI. ARBER (1925)

Both scutellum and coleoptile jointly = the single cotyledon.

VII. AVERY (1935)

1. scutellum = the single cotyledon ;
2. coleoptile (plumule sheath) = the second leaf ;
3. mesocotyl (the elongated structure between the scutellum and the coleoptile) = the first internode.

Date (*Phoenix sylvestris*, Fig. 162).

The seed is stony and cylindrical in shape. The outer brown layer is the testa. On the testa there is a longitudinal groove. In the middle of the opposite side of it there is a little protuberance, where the embryo is situated.

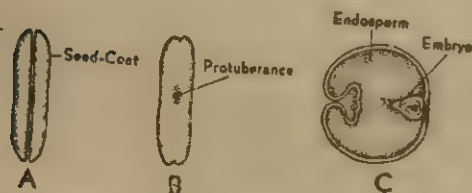


FIG. 162. STRUCTURE OF A DATE SEED

A; an entire seed ; B, front view of the same ;
C, the same cut crosswise.

On cutting the seed crosswise at this point, the embryo will be found embedded in the hard and horny endo-

sperm. The hardness of the endosperm is due to the presence of reserve cellulose in the thick cell wall.

Coconut (*Cocos nucifera*, Fig. 163).

The seed is rounded in shape. The hard stony covering, which is known as the *shell*, is not a part of the seed, but is the innermost part of the fruit cover (pericarp). On the shell there are three scars, popularly known as the *eyes*, and within one of them lies the minute undifferentiated embryo. On breaking the shell, the two coverings of the seed, *testa* and *tegmen*, are seen; the former is united with the innermost layer of the pericarp, while the latter is fused with the white fleshy endosperm containing reserve cellulose. The cavity of the endosperm is filled with a liquid, known as *milk*, which is an emulsion of fat and sugar.

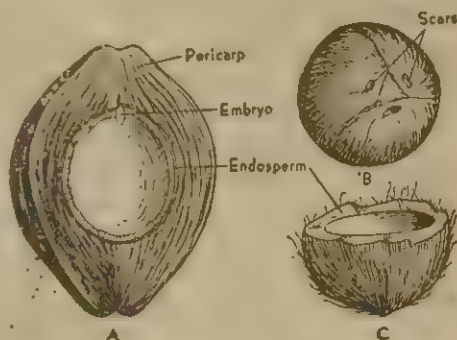


FIG. 163. STRUCTURE OF A COCONUT
A, an entire fruit cut lengthwise; B, an entire seed; C, the same split crosswise.

SEED GERMINATION

Germination is the process of awakening of the embryonic plant from the dormant state to active life and growth. In the term *germination* are included all the changes that take place in the dry seed from the time when it is placed under proper conditions up to its sprouting. The resumption of growth of the dormant embryo is called *seed germination*, and the tiny plant, produced as a result of germination, is known as a *seedling*.

CONDITIONS NECESSARY FOR GERMINATION

A. EXTERNAL FACTORS

For successful germination, the following external factors are essential, provided the seeds are viable:

Water. Water plays the most important part in the germination of seeds. It is necessary for (a) softening of the seed coats, and thus enabling the embryo to break through them more easily ; (b) swelling of the embryo as well as of the endosperm, which results in the bursting of the seed coats ; (c) facilitating the entrance of oxygen into the seed ; (d) diluting the protoplasm and permitting its various functions to go on actively* ; and (e) making possible the transfer of soluble foods from the endosperm or the cotyledons to the actively growing regions of the embryo, where they are necessary for the building up of the new formative material, the protoplasm.

Temperature. A suitable temperature is necessary for starting and continuing the process of growth, the range of temperature varying for different kinds of seeds. If the seeds be exposed to very low or high temperatures, they do not germinate. For every kind of seed there are minimum and maximum temperatures, below and above which germination will not take place. There is also an optimum temperature, at which the germination is at its best. Most seeds fail to germinate at a temperature as low as $0^{\circ}\text{--}5^{\circ}\text{C.}$, or as high as $45^{\circ}\text{--}48^{\circ}\text{C.}$ In most cases, the optimum temperature is $25^{\circ}\text{--}30^{\circ}\text{C.}$ The cardinal points of temperature for successful germination of the seeds are also variable with different samples of the same species.

Oxygen. Oxygen is necessary for an active respiration during the germination of a seed, as the embryo during its resumption of growth needs much more energy than is required by it in its dormant state, and this energy is only liberated by means of active and vigorous respiration. A few types of seeds have been found to germinate in the absence of oxygen, but they cannot complete the process.

Light. As regards the effect of light on germination, seeds may be *light-sensitive* (i.e., when germination is favoured by light), *light-hard* (i.e., when germination is inhibited by the effect of light), and *light-indifferent* (i.e., when the seeds germinate equally successfully irrespective of the presence or absence of light). As such, light probably plays a more important role in germination than was previously supposed.

*Living protoplasm cannot carry on its normal vital functions, such as digestion, respiration, assimilation, and growth, unless it contains a sufficient quantity of water.

B. INTERNAL FACTORS

A seed cannot germinate if its internal conditions are not satisfactory, though all the external conditions may be favourable. The following internal factors play important roles in the successful germination of seeds :

Presence of auxins. It has recently been discovered that some chemical substances, called **auxins** (*auxin a* and *auxin b*), are developed inside the seeds at the time of germination. In addition to these, another substance, known as **hetero-auxin**, which is a highly complex organic acid, has also been claimed by some investigators to be present in some seeds. These auxins are growth regulators in seedlings, and are analogous to hormones and vitamins in higher animals including man. They have rightly been called 'chemical messengers'.

Sufficient amount of reserved food. It has already been pointed out that the principal types of food matter, which are kept reserved in the seeds, are various kinds of carbohydrates, proteins, fats, and oils. These are absolutely necessary for normal growth and development of the seedling, because, these are sources from which the much-needed energy is obtained. Fats are more efficient storage foods than proteins or carbohydrates, since they liberate greater amount of energy per unit weight. Proteids are absolutely necessary, since they form an indispensable constituent of all living protoplasm.

Completion of dormancy. Dormancy (delayed germination) is a state or condition of relative rest and inactivity exhibited by a large number of seeds before they germinate. It is also a means of tiding over the period unsuitable for successful germination. Dormancy may be due to various causes, the important ones being (i) undeveloped embryo, as in *Ginkgo biloba*, (a gymnosperm), *Ranunculus* sp. (Fam. Ranunculaceae), *Corydalis* sp. (Fam. Fumariaceae), *Paris quadrifolia* (Fam. Liliaceae), etc. ; (ii) tough and thick seed coats preventing the easy absorption of water or retarding gaseous exchange, as in alfalfa (*Medicago sativa*) of S.F. Papilionaceae (Fam. Leguminosae), cocklebur (*Xanthium strumarium*) of Fam. Compositae, or rendering the embryos incapable of rupturing the seed

coats, as in water plantain (*Alisma plantago*) of Fam. Alismataceae, common pigweed (*Amaranthus* sp.) of Fam. Amaranthaceae, etc. ; and (iii) the necessity of 'after ripening' or slow and gradual chemical changes inside the embryo, as in hawthorn (*Crataegus oxycantha*) of Fam. Rosaceae. A seed becomes ready for germination after completion of a period of dormancy.

Viability (vitality) and longevity. Viability means the power or ability of the seed to germinate, while longevity denotes the length of time the seed can remain dormant and still be viable. Usually, the seeds retain their vitality for 5-6 years, while others remain viable only for a very short period.* Seeds of shepherd's purse (*Capsella bursa-pastoris*) and black mustard (*Brassica nigra*) of Fam. Cruciferae, chickweed (*Stellaria media*) of Fam. Caryophyllaceae, pigweed (*Chenopodium album*) of Fam. Chenopodiaceae, and some other weeds can germinate successfully after remaining buried in the soil for more than 30 years. Some leguminous seeds remain viable for about 50 years. The longest authentic case of longevity of seeds on record, however, is that of an Indian lotus (*Nelumbo nucifera*) of Fam. Nymphaeaceae, seeds of which, lain buried in a peat probably for more than 200 years, showed a very high percentage of germination. The chief factors which affect the viability and longevity of seeds are (i) parent vigour, (ii) conditions of exposure during development, (iii) degrees of maturation, (iv) conditions of storage, and (v) age of seeds.

CHANGES DURING GERMINATION

The principal physico-chemical changes which take place in the seed during germination are as follows :

Water intake. The starting point in the germination of a seed is the intake of water, which brings about the softening of the seed coats, the enlargement of the seed, etc. The water enters

*Very dry seeds, even when subjected to an extremely low or a very high temperature, retain their vitality. It has been noted that dry seeds of sugar-beet, even when placed at a temperature of -180°C . for half an hour, exhibit a very high rate of germination, while seeds of lotus also germinate very fairly when subjected to a temperature of $+103^{\circ}\text{C}$ for 16 hours. The majority of the dry seeds remain uninjured at a temperature between -10° to -20°C

into the seeds either by imbibition, or by osmosis, or by both.

Digestion. The insoluble stored food matters inside the seed are rendered soluble and diffusible by the process of *digestion*. This is brought about by certain digestive agents, which are known as *enzymes* or *ferments*. The enzymes are produced by the protoplasm itself, and, if kept under proper conditions of storage, can retain their activity though separated from protoplasm. They are very sensitive to temperatures. Very small quantities of enzymes are quite sufficient to bring about effective conversion without themselves being used up in the process, *i.e.*, they act as organic catalyzers. They are usually specific in their reactions. Although the exact composition of any of the enzymes has not yet been determined, yet broadly speaking, there are three main groups of enzymes, known as *carbohydratases*, *proteases*, and *lipases*, acting upon carbohydrates, proteins, and fats respectively.

Translocation of food. The transference of the digested food materials in a liquid state from the seat of digestion to the growing points (plumule and radicle) of a germinating seed is known as *translocation* of food. This translocation is effected almost entirely by diffusion from one living cell to another.

Assimilation. The incorporation of the digested foods into the body of the protoplasm itself is known as *assimilation*.

Respiration. Respiration is an oxidation process in which the complex food substances are broken down into much simpler compounds, like carbon dioxide and water, accompanied by a release of energy in the form of heat. So, it is an energy-releasing process as well. Respiration usually takes place in the presence of oxygen. It is very vigorous at the time of germination.

Growth. Growth is the permanent increase in bulk accompanied with permanent change of form. The growth of the embryo is due to the enlargement of cells already formed, and to the formation of new cells at the growing regions. The radicle and the plumule grow into the root system and the shoot system respectively.

TYPES OF GERMINATION

There are *three* types of germination, namely, *hypogeous* or *hypogeal*, *epigeous* or *epigeal*, and *viviparous*.

Hypogeous or hypogeal germination. In this type of germination, the cotyledon or cotyledons remain inside the seed coat, and never come above the soil. The plumule comes out of the seed coat usually by the elongation of the epicotyl, as well as, in some cases, by the growth of the base of the cotyledon. Thus, the original position of the cotyledon or cotyledons is not disturbed at all.

Examples :

Dicotyledonous exalbuminous, *e.g.*, pea*, gram, mango, *etc.*

Dicotyledonous albuminous, *e.g.*, custard apple, lotus, *etc.*

Monocotyledonous exalbuminous, *e.g.*, *Amorphophallus*,
Monstera, *Pothos*, *etc.*

Monocotyledonous albuminous, *e.g.*, paddy maize, wheat,
etc.

Epigeous or epigeal germination. In this type of germination, the cotyledon or cotyledons do not remain inside the seed coat, but come out above the soil. The plumule comes out of the seed coat by the elongation of the hypocotyl, and thus, the original position of the cotyledon or cotyledons is disturbed.

Examples :

Dicotyledonous exalbuminous, *e.g.*, bean, gourd, tamarind,
etc.

Dicotyledonous albuminous, *e.g.*, castor.

Monocotyledonous exalbuminous, *e.g.*, *Alisma plantago*.

Monocotyledonous albuminous, *e.g.*, onion, *Typha*, *etc.*

Vivipary or viviparous germination. (Fig. 164). The germination of the mangrove plants, which are chiefly found in the tidal marshes in Sundarbans, Sind (W. Pakistan), and Burma, as well as in salt lakes, is very peculiar. The seed, instead

*In some cases, epigeal germination may be noted in pea.

of being liberated from the fruit, germinates inside it while it is still attached to the parent plant. The embryo emerges out of the fruit with the massive hypocotyl pointing downwards. Afterwards, it falls vertically down into the mud beneath by its own weight, and fixes itself there by its pointed end. It is to be noted that the hypocotyl elongates according to the depth of water below, and when it is fixed into the mud, the embryo is kept above the surface of water. The common mangrove plants are *Rhizophora mucronata*, *Kandelia rheedii*, *Ceriops roxburghiana*, *Bruguiera gymnorhiza* and other plants belonging to Fam. Rhizophoraceae, *Avicenia officinalis* of Fam. Verbenaceae, *Ardisia humilis* and *Aegiceras majus* of Fam. Myrsinaceae, etc.*



FIG. 164. VIVIPARY IN *Ceriops*

GERMINATION OF A FEW COMMON SEEDS

A. DICOTYLEDONOUS SEEDS

Pea seed (*Pisum sativum*, Fig. 165).

When all the essential conditions for germination are satisfied, the plumule and the radicle start development. The radicle usually starts growth first, and it is the first structure to come out of the seed coat usually through the micropyle. It goes vertically downwards, and, after reaching the soil, produces the first or primary root, which gives rise to tiny secondary and tertiary branches in acropetal order, forming the root system. During

*Other instances of vivipary may be found in the following plants : (1) *Cassula* sp., (Fam. Compositae), found growing in the rice fields of Northern India ; (2) *Cometes surathensis* (Fam. Caryophyllaceae), found in Western Asia and Abyssinia ; (3) *Sechium edule* (Fam. Cucurbitaceae), cultivated for its edible fruit, which contains only one big seed ; (4) *Runusatia vivipara* (Fam. Araceae), an Indo-Malayan plant ; (5) *Poa*, *Festuca* and *Melocanna* of Fam. Gramineae ; and (6) *Cryptocoryne ciliata* (Fam. Araceae), found growing on the muddy banks of the Ganges.

development of the radicle, the epicotyl begins to grow, usually forming a loop, which afterwards straightens, and thus drags the plumule out of the cotyledons and the seed coat. The plumule develops rapidly giving rise to the true stem of the plant.

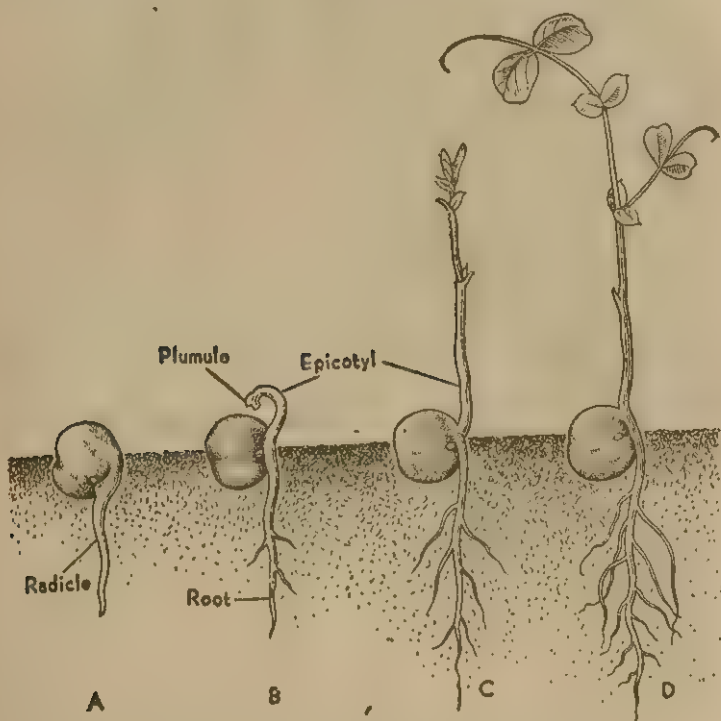


FIG. 165. GERMINATION OF PEA SEED

A—D, stages in germination.

as well as to the leaves, and gradually the shoot system is produced. During the whole process of germination, the cotyledons remain within the seed coat, and their original position is not disturbed at all. Hence, the germination is of the hypogeal type.* The cotyledons gradually diminish in size, afterwards wither and fall off.

*Occasionally epigeous (Priestley & Scott).

Tamarind seed (*Tamarindus indicus*, Fig. 166).

As in the case of the pea seed, the radicle grows first and forms the root system as usual. The primary root is conspicuous with a few secondary branches. During development of the root, the hypocotyl elongates considerably, forms a loop and finally

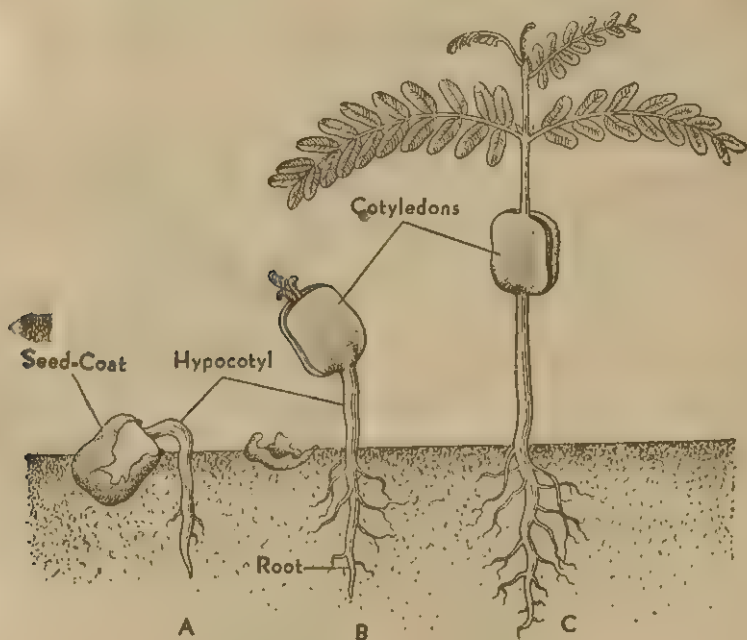


FIG. 166. GERMINATION OF TAMARIND SEED

A—C, stages in germination.

straightens, so that, the cotyledons are carried above the soil and are thus disturbed from their original position. The type of germination is, therefore, epigeal. Afterwards, the testa is cast off into small pieces, the cotyledons turn green in sunlight, manufacture food for the time being, and then may or may not separate. The plumule rapidly elongates and produces the shoot system as usual. The cotyledons gradually become smaller in size and subsequently fall off.

Gourd seed (*Cucurbita maxima*, Fig. 167).

The mode of germination is epigeal, as in the case of tamarind. But during development, the hypocotyl bends downwards, and soon a peg-like structure is formed on it. This one presses down the lower half of the testa, and thus helps the plumule to come out of the seed coat. The cotyledons, afterwards turn green, enlarge and form the first green leaves of the plant. The leafy cotyledons can be clearly distinguished morphologically from the ordinary green leaves.

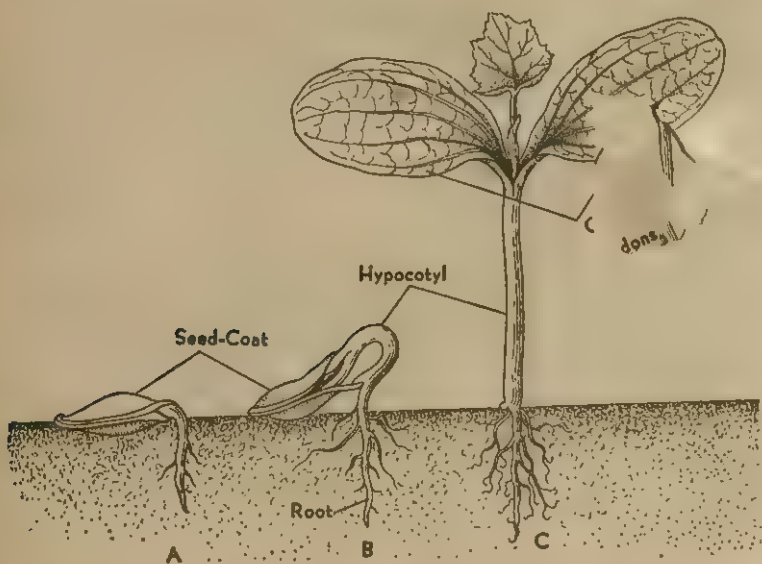


FIG. 167. GERMINATION OF GOURD SEED
A—C, stages in germination.

Castor seed (*Ricinus communis*, Fig. 168).

The germination of castor seed is somewhat similar to that of tamarind, except that the cotyledons are thin and leafy structures, which function first as absorbing organs and later as true leaves. The endosperm of the seed is carried up above the soil along with the cotyledons owing to rapid development of the hypocotyl. The cotyledons are at first engaged in absorbing food

from the surrounding endosperm till it has almost entirely been consumed. Finally, they separate and the remaining portion of the endosperm gradually dries up and then falls off. The cotyledons, as usual, enlarge, become green and manufacture some amount of food for a considerable length of time. But the deve-

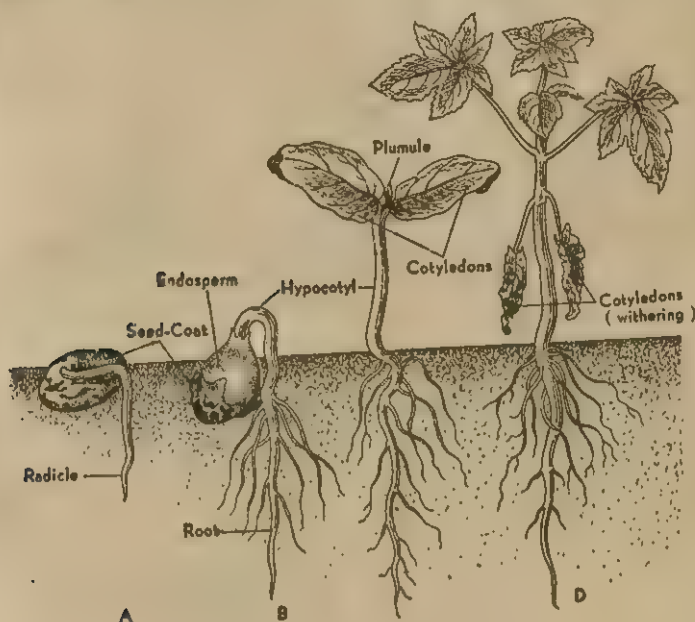


FIG. 168. GERMINATION OF CASTOR SEED
A—D, stages in germination.

lopment of the plumule is very slow, and when the shoot system develops from it, the cotyledons dry up and fall off.

B. MONOCOTYLEDONOUS SEEDS

Maize (*Zea mays*, Fig. 169).

The germination of maize may be taken as typical of all cereals, such as paddy, wheat, oat, *etc.*, and other grasses. The epithelial layer of the scutellum absorbs digested food from the surrounding endosperm and transfers it to the growing embryo.

The coleorhiza comes out first still enclosing the radicle, and, on coming in contact with the soil, produces some hairy structures. The radicle gradually breaks through the coleorhiza and the fused common wall of the seed coat and the pericarp, forming the primary root. Almost simultaneously with its development, usually three seminal roots (Fig. 170) appear from above the radicle.

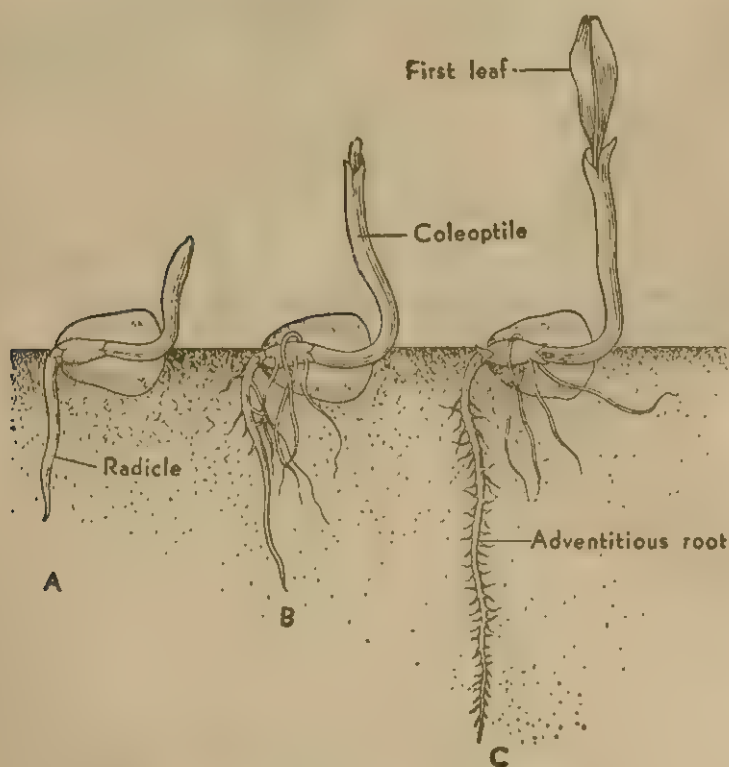


FIG. 169. GERMINATION OF MAIZE GRAIN

A—C, stages in germination.

Adventitious roots begin to develop very rapidly from the hypocotyl. Eventually, an extensive fibrous root system develops and fibrous roots also develop from a few lower nodes of the shoot ; the primary root usually dies after a short duration. Later on,

during development of the root system, the plumule, covered by the coleoptile, emerges from the grain as a smooth conical upgrowth which often reaches a length of about 25.4 mm. Through the tip of the elongated coleoptile the first green leaf tears its way. In this way, the shoot system is established. The grain with the endosperm and the adpressed cotyledon (scutellum) remains within the common fused coats, and the original position of the seed is not disturbed at all. Therefore, the type of germination of the seed is hypogeal. As germination proceeds, the grain becomes softer indicating the utilization of the stored food by the germinating embryo, and after the establishment of the seedling, the remnant of the seed gradually decays in the soil.

Date (*Phoenix sylvestris*, Fig. 171).

With the commencement of germination, the cotyledon secretes an enzyme, by means of which the reserve cellulose inside the horny endosperm is rendered soluble. The cotyledon absorbs it and begins to enlarge. The upper portion of the cotyledon remains within the endosperm absorbing food matters, while the lower portion (sheath and stalk) comes out carrying the plumule and the radicle within it. Then the radicle elongates, grows vertically down into the soil, and produces the primary root, which branches and is more strongly developed (unusual in monocotyledons), but it does not give rise to a root system. By this time, the plumule pierces the tubular sheath of the cotyledon on one side, rises upwards, and produces leaves. The lower end of the axis of the shoot produces many adventitious roots. The mode of germination is hypogeal.

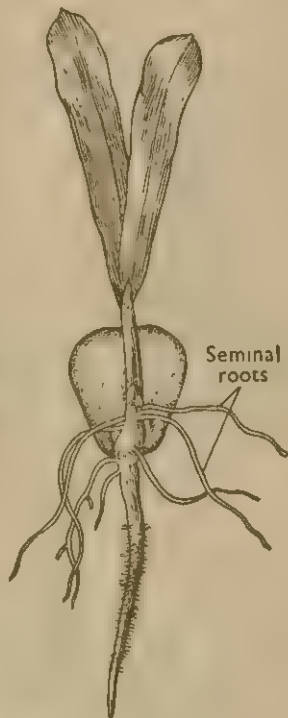


FIG. 170. SEMINAL ROOTS OF MAIZE.

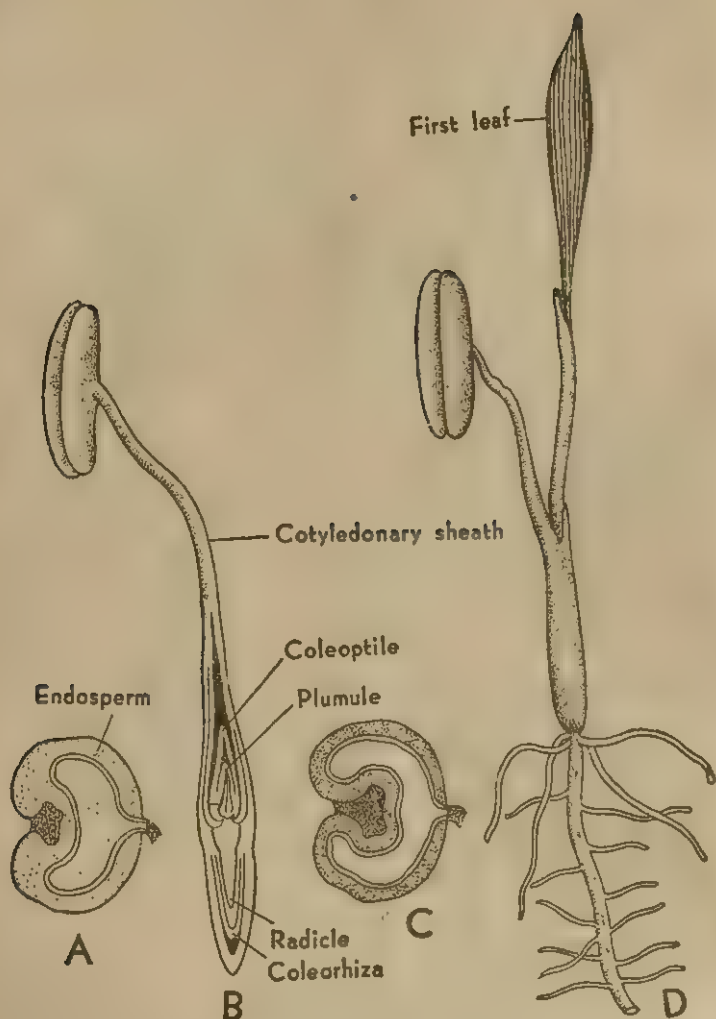


FIG. 171. GERMINATION OF DATE SEED
A—D, stages in germination.

Coconut (*Cocos nucifera*, Fig. 172).

When germination begins, the cotyledon gradually becomes larger and spongy in nature, ultimately occupying the whole cavity within the endosperm. The spongy cotyledon absorbs food matters. In this case, no sheath is formed, as in the other members

of the Fam. Palmae, and the embryo germinates *in situ*. The adventitious roots develop from the lower end of the axis, spread out



FIG. 172. GERMINATION OF COCONUT
A—C, stages in germination.

on all sides of the shell, emerge through the fibrous covering of the fruit, go down into the soil, and ultimately form the root system. The shoot is developed from the upper end of the embryo, which ultimately produces stem and leaves, but no branches. The mode of germination is hypogeal.

Onion (*Allium cepa*, Fig. 173).

During germination, the radicle elongates, grows vertically into the soil and forms the primary root, but afterwards it dies and is replaced by adventitious roots, developed from the base of the stem. The lower part of the cotyledon also elongates and grows out of the testa forming a loop or arch, like the hypocotyl of the tamarind, and then comes above the soil and forms the first green leaf of the plant. The tip of the cotyledon remains coiled up inside the testa for absorbing food matters from the endosperm. Later on, the plumule pierces through the base of

the cotyledon and produces new leaves. The mode of germination is epigeal.

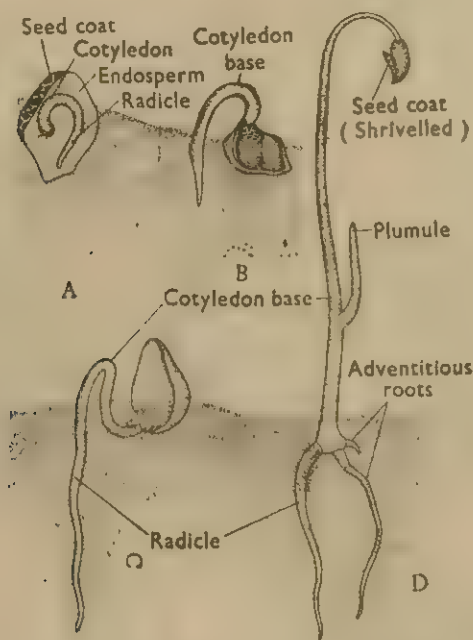


FIG. 173. GERMINATION OF ONION SEED
A—D, stages in germination.

Differences between dicotyledonous and monocotyledonous seeds

Dicotyledonous seeds

Monocotyledonous seeds

(a) As regards structure

- | | |
|--|--|
| 1. Seed coats are usually free from the pericarp. | 1. Seed coats are usually fused with the pericarp in albuminous seeds. |
| 2. Embryo is comparatively large and possesses two cotyledons. | 2. Embryo is minute and possesses one cotyledon only. |
| 3. Plumule and radicle are not covered by any sheath. | 3. Plumule and radicle may be covered by coleoptile and coleorhiza respectively. |
| 4. Plumule is terminal and cotyledons are lateral. | 4. Plumule is lateral and cotyledon is terminal. |
| 5. Exalbuminous or albuminous. | 5. Usually albuminous. |

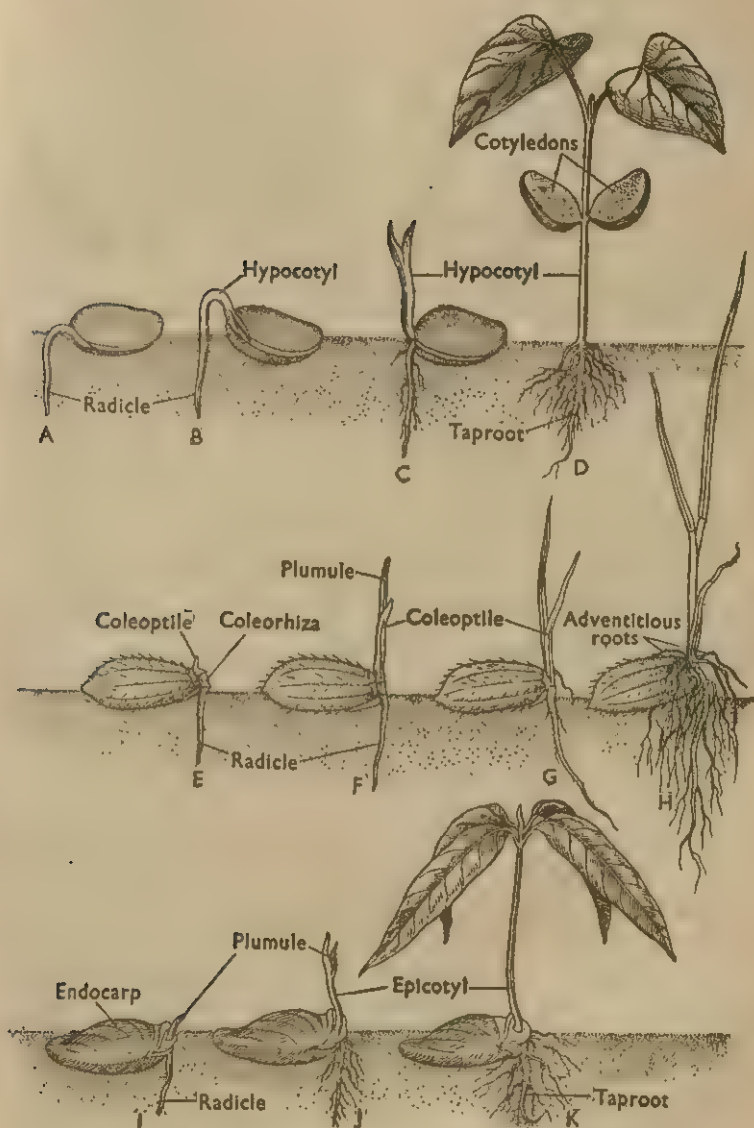


FIG. 174. DIFFERENT STAGES OF GERMINATION IN BEAN (A—D), PADDY GRAIN (E—H), AND MANGO SEED (I—K).

Dicotyledonous seeds

Monocotyledonous seeds

(b) As regards germination

- | | |
|---|--|
| 6. Radicle does not pierce any sheath. 7. Plumule comes out of the seed by the bending of the epicotyl or hypocotyl. 8. Radicle produces the primary root, which is persistent; the primary root produces copious secondary and tertiary roots. 9. The mode of germination is hypogeal or epigeal. | 6. Radicle forces its way through coleorhiza (when present). 7. Plumule comes out after piercing the coleoptile (when present). 8. Radicle produces the primary root, which is usually soon replaced by adventitious roots. 9. The mode of germination is usually hypogeal. |
|---|--|

FUNCTIONS OF COTYLEDONS

The cotyledons usually perform the following functions :

They protect the plumule. In exalbuminous seeds, they act as store-houses of food substances. In albuminous seeds, they absorb food from the endosperm and supply it to the growing embryo. When germination is epigeal, they become green and form the first leaves, and thus help in photosynthesis. In some monocotyledonous seeds, e.g., palmyra palm, date, etc., the cotyledon helps the plumule and the radicle to come out of the seed coat, while in other cases, as in coconut, it acts as a sucker for the absorption of endosperm.

ECONOMIC IMPORTANCE OF SEEDS

Of all parts of the plant body, the seeds form the most important sources of staple food supply. The value of the three outstandingly important cereal crops, namely, rice, wheat and maize, needs no introduction. Other important crops, providing food both for the human beings as well as for the cattle, are millet, barley, oat, sorghum, rye, etc. These are more or less cultivated all over the world. Seeds of the leguminous plants have also very great economic importance. They give us pulses (lentils, peas, grams, etc.), soy beans (*Glycine soja*, and *G. hispida* belonging to S.F. Papilionaceae of Fam. Leguminosae), pea nuts, beans and others, all of which are rich sources of vegetable proteins. Various kinds of nuts, like walnut, chestnut, cashewnut, coconut, almond, etc., are also

used for food. The coconut is also the source of copra, its dried meat, from which an oil is extracted. Seeds of flax, linseed, cotton, tung-oil seed, *etc.*, yield important oils used in the paint and varnish industries. Oils extracted from the seeds of mustard, groundnut, coconut, linseed, *etc.*, are used for domestic purposes. Castor oil, from seeds of castor, is used as medicine as well as an engine-lubricant and a fuel. The seeds of *Taraktogenos kurzii* (Fam. Bixaceae) yield the famous chaul-moogra oil, which is extensively used in the treatment of leprosy and other cutaneous diseases. Coffee bean of commerce is obtained from the seeds of *Coffe arabica* (Fam. Rubiaceae), a plant widely cultivated in the tropical regions of the world. Various kinds of alcoholic drinks are usually prepared from the cereals. Seeds, like cotton, are very good sources of fibres, which are not only used in the textile industry, but also provide important materials necessary in the manufacture of explosives, tyres, celluloid, rayon, cellophane, *etc.* Kapok seeds are used for stuffing pillows, mattresses and furniture. Some important dyes like anatto, used in dyeing and staining butter, are obtained from the seeds of *Bixa orellana* (Fam. Bixaceae). Sometimes, the oils from the seeds of *Guizotia abyssinica* (Fam. Compositae), *Argemone mexicana* (Fam. Papaveraceae), *Madhuca latifolia* (= *Bassia latifolia*) of Fam. Sapotaceae, *etc.*, are extensively used by unscrupulous dealers in adulterating edible oils and clarified butter. Jewellers use the red seeds of *Abrus precatorius* of S.F. Papilionaceae (Fam. Leguminosae) as small weights. Endosperm of the tropical American genus *Phytelephas* (Fam. Palmae) yields vegetable ivory.

PART II
ANATOMY



CHAPTER I

THE CELL

Though the foundation stone of the present-day concept of cell as the 'basic unit of life' was laid down with the invention of the compound microscope by J. and Z. Janssen (1590), two Dutch spectacle-makers, it was Robert Hooke (1665), an English engineer, who first studying a thin slice from an ordinary bottle cork and noting the presence of numerous small cavities resembling the compartments of a honeycomb within it, coined the term 'cell'. He published his observations in his classical book '*Micrographia*'. He had, however, no clear idea regarding the cell contents, but from his later studies, spoke of some sort of nourishing juice present in the cells.

Later on, Marcello Malpighi (1675), an Italian Professor of medicine, and Nehemiah Grew (1682), an English physician, worked out in detail the forms and arrangements of cells in different parts of the plant body. These pioneer workers, however, failed to observe the presence of protoplasm within the cells. Evidently, their attention was confined to the walls surrounding the cavities, which signified the cells.

Robert Brown (1831), an English botanist, while working with orchid leaves, observed that in each of the epidermal cells there was a single, somewhat granular and centrally placed circular structure, to which he gave the name '*nucleus*'.

Dutrochet (1824), a French biologist, first considered the cells as definite morphological entities, but he concentrated his studies more on the cell wall than on the actual cell contents.

A great scientific enunciation was put forward in 1839 by M. J. Schleiden and T. Schwann, two German scientists, the former a botanist and the later a zoologist. The *cell theory* or the *cell doctrine* pronounced by them was acclaimed as a hallmark in the study of modern biology. They believed that all organisms are composed of essentially similar parts, the cells, which are the elementary living units, and whose united action determines the development of an organism. In other words,

they regarded the cell as the primary agent of organization. According to the founders of the cell theory, who had no better idea than Dutrochet as to the nature of the cell contents, these were considered to be of little importance. About twenty years later, another great announcement was made by R. Virchow (1858), a German physician, that cells never arise *de novo*, and only pre-existing cells can give rise to new ones.

The protoplasm of the cell was first observed by Corti (1772), and Dujardin (1835) noted its constant occurrence in every living cell. Von Mohl (1846) recognized that each living cell contains some semi-fluid granular substance and considered it to be the first-formed cell content; the term '*protoplasm*' was first applied to it by him. This put the cell theory on a much stronger foundation.

Sometimes later, Schultze (1861) established the *protoplasm doctrine*, which stated that the units of organization are masses of protoplasm, which are generally similar in all living organisms. He described the cell as a mass of protoplasm with a nucleus, and stated that each cell arises by the division of a pre-existing cell. The cell was thus primarily the organized protoplasmic mass, termed '*protoplast*' by Hanstein (1880). The cell wall then came to be of secondary importance only. Huxley (1868) happily expressed this material substratum of life processes as the '*physical basis of life*'.

As opposed to the cell theory, the *organismal theory*, developed and supported by de Bary (1862), Hofmeister (1863), Sachs (1882) and others, emphasizes that a multicellular organism is not merely a colony of individual and isolated cells, but rather a continuous mass of protoplasm, which has become divided into different centres of action, the cells, during development. In this case, growth does not mean multiplication of elementary units to form a new whole, but rather differentiation of the growing protoplasm into newly formed metabolic units. Thus, according to the cell theory, in case of coenocytes, each nucleus with the portion of cytoplasm influenced by it, represents a cell. On the other hand, according to the organismal theory, the whole multinucleate body is a huge cell. Whether adherents to the cell theory or to the organismal theory, all, however, agree that the various life processes noted in an organism from its birth to its

death are nothing but different aspects of diverse performances by the various cells.

GENERAL CONSIDERATION OF THE CELL

If a thin slice or section (Fig. 175) is made from any living part of the plant body and examined under a compound microscope, it will be found that the section* is composed of a large number of united and more or less rounded or polygonal compartments

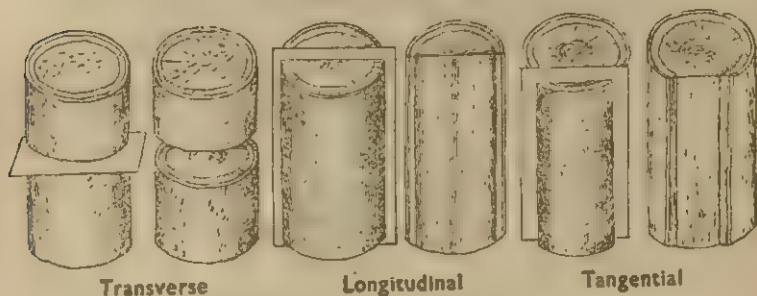


FIG. 175. DIFFERENT PLANES OF MAKING SECTIONS OF PLANT ORGANS

(Fig. 176), each of which consists of a space surrounded by a wall. On closer examination, it will be found that the space within each compartment is occupied by a semi-transparent, viscous fluid, known as **protoplasm**. This protoplasm is the living substance of the plant, and each organized unit mass of protoplasm in each cavity is called a **protoplast**. The protoplast with its surrounding wall, the **cell wall**, is termed a **cell**. The cell wall is a dead substance and is regarded as a secondary product formed by the vital activity of the protoplasm for its protection and stability ; it acts as a framework giving form, firmness and strength to the cell. It is not an essential part of the cell, since in some cases, it may be entirely absent, as in the reproductive cells (e.g., spermatozoids, zoospores, etc.) ; such a protoplast is said to be *naked*. The protoplasm is the most essential part of a living cell, since life could never exist apart from it. When the protoplasm disappears from a cell, it is said to be *dead* and

*In some plants of lower groups, the cellular structure can be studied directly under the microscope without preparing any section.

the skeleton or framework, the cell wall, is left behind. Thus, the section in question is composed of several cells, and the plant body is made up of millions of such cells. These cells are the structural units of the plant body in the same sense as bricks

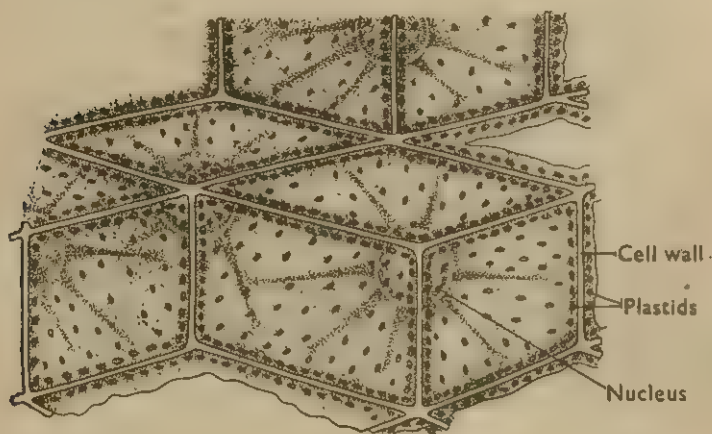


FIG. 176. A GROUP OF CELLS (*three-dimensional diagrammatic figure*)

are the structural units of a brick edifice. The cells are also regarded as the functional units, since all the activities of the plant are carried on by the cells themselves. Every cell performs a definite physiological function, either for the whole term of its existence or, at any rate, for some period of its life. A cell may thus be defined as *a structural as well as functional unit* of the plant body.

A living organism always starts its life as a single cell. If it remains one-celled throughout its whole term of life, it is said to be **unicellular**. On the other hand, if the organism becomes many-celled during the course of its development, such an organism is said to be **multicellular**. The lowest forms of plants are unicellular, *e.g.*, yeast, bacteria, diatom, desmid, *etc.* These plants are usually microscopic and are hardly visible to the naked eye. It is to be noted that the same cell in a unicellular plant carries on all the necessary functions of life. All the higher forms of plants are multicellular. In the lowest forms of multicellular plants, the plant body consists of almost similar cells which carry on more or less similar function, but in case of higher plants,

there is a more or less complete physiological division of labour, and the cells are of different kinds and combine in various ways to perform different functions.

The cell shape varies extremely, depending on the pattern of the body of the organism as well as to its diverse life processes, both these factors being governed to a considerable extent by the environment in which it lives. Similarly, the cell size is also widely variable, the smallest-sized cells being found amongst the bacteria ($0.2-5.0\mu$).^{*} The size of a cell depends on three major factors, namely the metabolic rate of the cell, the ratio of the surface area of the cell to its volume, and the ratio of the cytoplasm to the nucleus in the cell.

There is no such cell, which can be regarded as a typical or representative one. A so-called typical adult plant cell (Figs. 177 & 178), however, consists mainly of two parts: *protoplasm* and *cell wall*. The protoplasm mainly includes the nucleus and the cytoplasm, as well as plastids, chondriosomes or mitochondria, golgi bodies, centrosomes, vacuoles, and ergastic substances. The wall bounding the protoplasm is the cell wall. Hanstein (1880) suggested the term '*protoplast*' to denote an organized unit mass of protoplasm contained within a single cell.

A brief account of the protoplasm is given in the following pages, while the cell wall has been discussed in the next chapter.

PROTOPLASM

Protoplasm, the living matter, which is so conspicuous and universally distributed in every living cell, was justly described by Huxley as the '*physical basis of life*'. It cannot be stated what protoplasm really is. Wilson says, "the ultimate basis of living matter is not a single chemical substance, but a mixture of many substances that are self-propagating without the loss of their specific characters." Thompson states, "protoplasm is a marvellous form of matter in motion, of which we can form only a very vague conception."

^{*} $1\mu = \frac{1}{1000}$ mm.

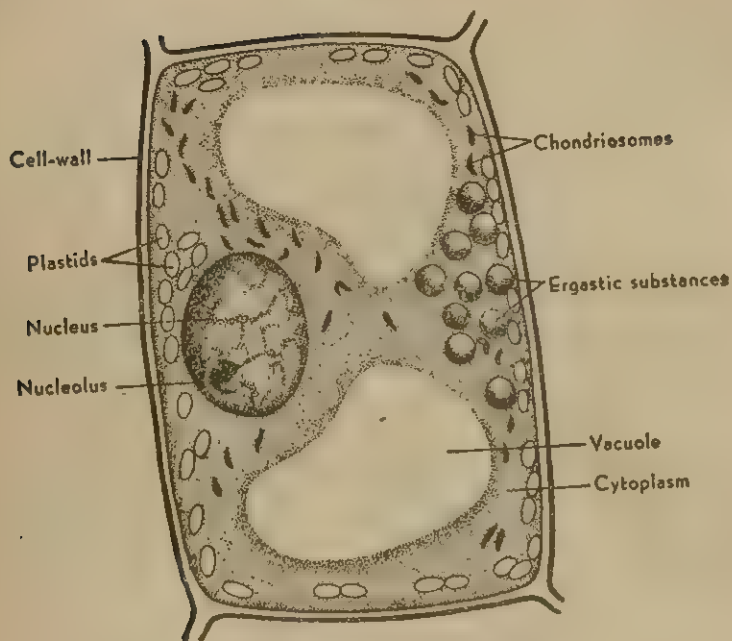


FIG. 177. A MATURE PLANT CELL

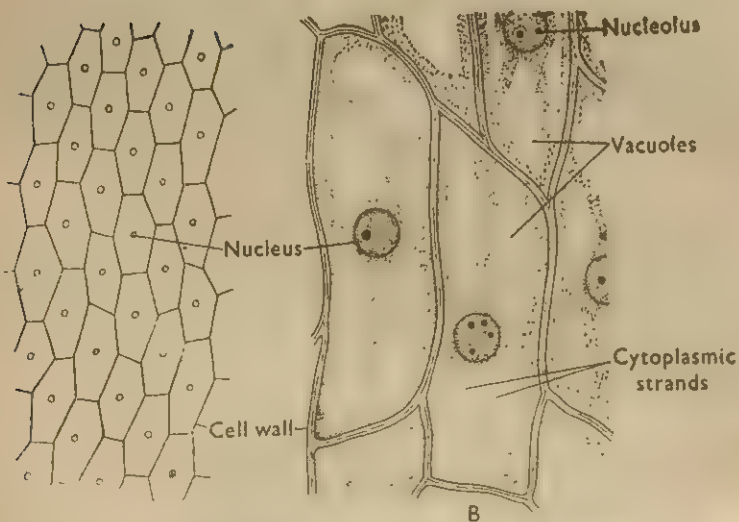


FIG. 178. CELLS FROM THE SCALE LEAF OF ONION

A, a group of cells under low power ; B, a few cells magnified.

Physically, protoplasm is a colloidal, viscous, elastic, semi-transparent, jelly-like fluid, somewhat granular in character and saturated with water ; its density varies in accordance with the quantity of water present in it. When deprived of its component water, the protoplasm, without losing its vitality, gradually ceases to perform its vital functions and becomes hard and tenaceous. This is particularly evident in case of dry seeds, which, when supplied with a suitable quantity of water, revive again due to the awakening of the dormant protoplasm.

Earlier workers advanced several theories to explain the structure of protoplasm. Briefly, they may be summarized as follows :

1. **Reticular theory** (Frommann, 1765-84)—protoplasm is a reticulum or very fine network of a more or less solid substance holding a fluid or some granules in its meshes.
2. **Fibrillar or filar theory** (Velten, 1873 ; Flemming, 1882)—protoplasm consists of the fine fibrils (*mitomes*), very often branching, but never forming a network, and bathed in a fluid (*paramitome*).
3. **Granular theory** (Altmann, 1886)—protoplasm consists of innumerable minute granules, elementary living units or *bioblasts*, contained in a liquid, non-living *hyaloplasm*. The cell is thus an assemblage of bioblasts.
4. **Alveolar or emulsion or foam theory** (Butschli, 1892)—protoplasm consists of minute droplets of a liquid suspended in another continuous liquid like an extremely fine emulsion.

In the light of our present knowledge, protoplasm may be regarded as a complex colloidal gel—a complex system of various substances dispersed in the form of granules, globules, filaments and networks, thus exposing an enormous area of reacting surface in proportion to the volume. It is a living system of components, which by themselves are non-living ; the parts play their role because of their position in the system as a whole.

Chemically, protoplasm is not a simple substance, but it is rather very complex in its composition. It is very difficult to get an exact composition of the protoplasm. Whenever we go to analyze protoplasm, it becomes dead, and the composition of the dead protoplasm is quite different from that of the living one. However, it may be said that various substances, such as proteins and their derivatives, lipoids, carbohydrates and inorganic salts, together with a large amount of water, enter into the composition of the protoplasm, and these contain the following chief elements : carbon, hydrogen, oxygen, nitrogen, sulphur, and sometimes phosphorus. Water forms the main bulk, nearly 70 to 90 per cent of the total volume. The continuous phase (dispersion medium) is a solution of various inorganic salts, e.g.,

nitrates, phosphates, sulphates, chlorides, *etc.* The dispersed phase consists mainly of the organic compounds such as, proteins, fats and carbohydrates. Proteins consist mainly of carbon, hydrogen, oxygen, nitrogen, sulphur, and phosphorus. Fats and carbohydrates consist of carbon hydrogen, and oxygen, in varying proportions. Sugar, starch, cellulose, glycogen, *etc.*, are the common carbohydrates. When burnt, protoplasm emits the smell of ammonia. Active protoplasm gives slightly alkaline or neutral reaction, but never an acid one. Protoplasm undergoes coagulation, like the white of an egg, on the application of alcohol, dilute mineral acids and also heat (at about $54.5^{\circ}\text{C}.$). But, in an inactive dried condition, it can withstand a higher temperature without coagulation, as in the case of seeds and spores.

Living protoplasm, wherever existing, either enclosed by a cell wall or not, is in constant motion. The cytoplasm of the vegetable cell which possesses a distinct cell wall often displays a more or less streaming movement, which is usually known as

cyclosis (Fig. 179). This streaming

movement is of two kinds : **rotation**—when the stream flows uniformly round the inner surface of the cell wall having the direction of the stream constant, as in the cells of *Vallisneria* ; and **circulation**—when the path of the stream has a more or less complicated course due to the direction of the stream undergoing reversal, as in the cells of the staminal hairs of *Tradescantia*. Rotation is commonly found in aquatic plants, while circulation is characteristic of terrestrial ones. Besides these, there are two other kinds of protoplasmic movements, which are exhibited by the naked protoplast only. These are known as

amoeboid and **ciliary** movements. The movement is spoken of as amoeboid, when the whole naked mass of protoplasm assumes irregular, constantly changing shapes, and performs creeping movement like the unicellular animal amoeba.



FIG. 179. CYCLOSIS
A, rotation ; B, circulation.

plasm assumes irregular, constantly changing shapes, and performs creeping movement like the unicellular animal amoeba.

This type of movement is well-illustrated in the vegetable kingdom by the plasmodium of a slime mould (Fig. 180).



FIG. 180. PLASMODIUM OF SLIME MOULD.

The movement is said to be ciliary, when the naked mass of protoplasm, having its parts prolonged into one or more whip-like vibratile processes, called *cilia* or *flagella*, moves to and fro with the help of these structures. This is exhibited by the reproductive cells, such as zoospores, spermatozooids, *etc.*

Protoplasm performs all the necessary functions of life, since it is the physical basis of life. The process of nutrition and other chemical actions are carried on by the protoplasm. It is in the protoplasm also that interchange of energy occurs, which becomes necessary when translocation of materials takes place. Further, that remarkable property of the living organism, which the physiologists call irritability, resides in the protoplasm. It alters the nature of the substances which enter into it and recombines them into a substance like itself. Finally, it is the protoplasm which initiates and carries out all the processes concerned in reproduction.

Tests : (1) It turns brownish-yellow with iodine solution. (2) When boiled with nitric acid, it turns yellow, which, when cooled and ammonia

added, becomes orange (*Xantho-protein test*). (3) It turns brick-red when boiled with nitrate of mercury or Millon's reagent (*Millon's test*). (4) With sulphuric acid and cane sugar, it gives a rose-red colour. (5) It dissolves and becomes perfectly transparent in caustic potash and eau-de-javelle (an aqueous solution of sodium hypochloride).

All the aforesaid reagents kill the protoplasm, and these characteristic reactions are only manifested when the protoplasm becomes dead. Living protoplasm does not usually take up the stains except with a few 'vital stains', such as neutral red and Janus green.

NUCLEUS

The nucleus is a highly specialized and differentiated part of the protoplasm found somewhere in the cytoplasm of the cell. It is a highly individualized organ, and is found to occur nearly in all living vegetable cells, except in the very lowly organized groups of plants, such as Myxophyceae (blue-green algae) and bacteria, where the nuclei of the normal type have not yet been demonstrated. But the chromatin granules, which are found to occur in Myxophyceae, are supposed to perform, at any rate, some of the functions of the nucleus.

Usually, there is only one nucleus in a cell, and such a cell is called **uninucleate**. But there are some cells, which contain many nuclei, and these are said to be **multinucleate**, as in fungi, some algae, certain reproductive cells, and some abnormal cells of seed plants, abnormalcy being due to age, disease or injury. The multinucleate condition may arise in two divergent ways: either by the division of the original nucleus, or by the absorption of the walls of adjoining cells, as in the case of latex vessels. In some cases, a single cell may grow into an extensive much-branched, aseptate body containing innumerable nuclei, developed by the repeated divisions of the nucleus of the mother cell, distributed in the general mass of continuous cytoplasm. Such a body is a **coenocyte**, as is found in some algae (e.g., *Vaucheria*) and fungi (e.g., *Mucor*).

Typically, nucleus is spherical or ellipsoidal in form. In some cases, it may be elongated dumb-bell-shaped, crescent-shaped, etc. Their size may vary from 1μ (e.g., in *Mucor*) to 600μ (e.g., in the egg cell of *Dioon*, a gymnosperm) in diameter, but having an average diameter of 5.25μ . Nuclei are usually large in some monocotyledons and conifers, while these are remarkably

small in fungi. In young meristematic cells, these are very conspicuous and appear large owing to the relatively small size of the cells. But, when a cell gradually increases in size, there is no corresponding increase in size of the nucleus, and hence, in an adult cell it appears comparatively small and occupies a lesser space than in the young cell.

The nucleus usually lies at the centre of the cell. When there are a number of small-sized vacuoles, the nucleus is generally seen to occupy a central position; but, when there is a large central vacuole, the nucleus lies either at the peripheral layer of the cytoplasm or at the centre of the vacuole. In the latter case, the nucleus remains connected to the peripheral cytoplasm by means of cytoplasmic strands.

Chemically, the nucleus much resembles the protoplasm and consists of carbon, hydrogen, oxygen, sulphur, and an enormous quantity of phosphorus. It always contains a nucleoprotein, known as *nuclein*, consisting of nucleic acid and a protein base, such as protamine, histone, etc.

The nucleus can never be formed *de novo*. It always originates by the division of the pre-existing nucleus, either directly (amitosis) or indirectly (karyokinesis or mitosis). In amitotic division, the nucleus divides into two parts by simple constriction, and naturally, may not result in the formation of two daughter nuclei of equal size. This process results in the formation of several nuclei within the mother cell, which becomes multinucleate, or those divisions are followed by wall-formations in between the nuclei forming new cells. Examples of amitosis are chiefly found in lower plants, particularly in the internodal cells of *Chara*.*

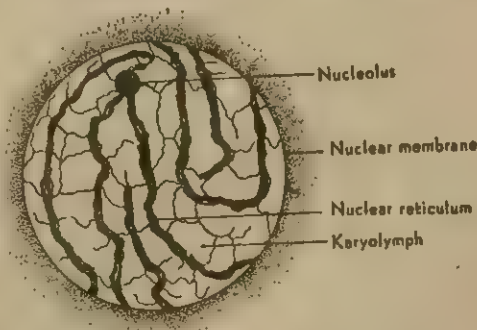


FIG. 181. STRUCTURE OF NUCLEUS

*For details of indirect division, refer to Part III.

The nucleus (Fig. 181) presents a sac-like appearance surrounded by a distinct, delicate membrane containing within it a network of delicate threads. In a properly fixed and stained preparation, the nucleus in its resting or 'metabolic' condition (not dividing) has the following structural elements :

The nuclear membrane. It is definitely a protoplasmic membrane, which separates the nucleus from the surrounding cytoplasm. Some cytologists are of opinion that it is a distinct morphological structure formed by the action of materials between nucleus and cytoplasm. This membrane is a double-layered structure composed of proteins and lipids.

Karyolymph or nucleoplasm. It is the dense, jelly-like, hyaline, protoplasmic ground substance, which fills up the nuclear cavity and with which the meshes of the nuclear reticulum are filled. It is also known as the **nuclear sap** or **nucleohyaloplasm**. It acts as a storehouse of reserve materials to be used up during nuclear division.

Nuclear reticulum. It is the main mass of the nucleus and consists of an irregularly branched network of delicate threads with beads of coarser granules lying in the nuclear cavity. This network is the **chromatin**, a highly stainable substance, which appears more clearly as the chromosomes, the bearers of the hereditary characters, during cell division. In each nucleus the chromosomes occur in a definite number. The coarser granules are the **chromocentres**, which stain more deeply than the rest of the network. Chemical analyses reveal that there are four major molecules organized together to give rise to the chromatin. These are *histone* (a protein), a more *complex protein*, *deoxyribose nucleic acid* (DNA), and *ribose nucleic acid* (RNA). Of these four, DNA, the key molecule, in its turn, is composed of a number of smaller linked-up molecules including *deoxyribose* (a sugar), *phosphoric acid*, *thymine*, and *cytosine* (both *pyrimidine* bases), *adenine* and *guanine* (both *purine* bases).

Nucleolus. There is a very distinct, dense, highly refractive and stainable, spherical body lying within the nucleus, which is its *nucleolus*. A particular chromosome forms the nucleolus at a special region, called the **nucleolar organizer**. Usually, the number of nucleolus in a nucleus is fixed, but it may vary. The exact function of the nucleolus is not yet known. It, how-

ever, seems to be related to the manufacture of proteins. Further, as it is made up of proteins and RNA, it may be connected with the phenomenon of transference of genetic materials and information from the nucleus to the cytoplasm. In some plants, ephemeral vacuoles are found within the nucleolus; these are termed as **nucleolar vacuoles**, which take a few minutes to be fully formed, and then disappear within a few seconds.

The nucleus appears to be the controlling centre of all the activities of the protoplast and plays an important part in the constructive metabolism of a plant. It also exerts a direct influence on the growth and differentiation of the cell, hence, it is regarded as 'the brain of a cell'. The nucleus is also regarded as the bearer of the hereditary characters, *i.e.*, through it the characters of the parents are transmitted to the offspring. The breaking of the reticulum into chromosomal elements with great precision and their equitable distribution into two daughter nuclei during somatic cell division, synapsis and halving of the chromosome number during reduction division, and nuclear fusion associated with the doubling of the chromosomes in case of gametic union, all point to the nucleus as the bearer of inheritable characters.

CYTOPLASM

The cytoplasm is a more or less transparent, viscous, colourless fluid and forms the general mass of protoplasm omitting the nucleus. It forms the greater part of the protoplasm and completely fills up the space within a young cell.

The cytoplasm consists of a basic hyaline substance, known as **hyaloplasm**. When it becomes granular and forms the general mass, it is called the **endoplasm**. This endoplasm is bounded at the periphery by a very thin hyaline layer of plasma entirely free from granules, and forms the **ectoplasm** (**plasma membrane***), which separates the endoplasm from the adjacent cell wall. A similar thin hyaline layer of cytoplasm surrounds each vacuole, and is termed the **tonoplasm**.† All the granular substances in the endoplasm are collectively termed as **microsomes**.

*Some botanists question the presence of such a plasma membrane in the cells of the higher plants, but its presence in some lower organisms is unquestionable.

†Termed by Hugo de Vries.

The cytoplasm is mainly concerned with rendering some sort of service, like transmission of messages, affording protection, causing movement, *etc.*, or with giving rise to some product, like a pigment, a storage material, and even new cells, or with both together.

PLASTIDS

The plastids are small, granular, definite, living bodies, which are highly specialized and conspicuous inclusions of the cytoplasm. The body of the plastid is known as the **stroma**. The total plastid complex of an organism of a cell is sometimes referred to as the **plastiodome** (Dangerad, 1935).

Plastids are almost of universal occurrence excepting fungi, bacteria, slime moulds, and blue-green algae. In meristematic cells, there are extremely minute, more or less rounded, colourless bodies, which are found lying embedded in the cytoplasm round about the nucleus. In size, they are usually small, having an average diameter varying from $4-6\mu$; these are termed the **proplastids**, the smallest being at the limit of the microscopic visibility. As the cells mature, the proplastids multiply and develop into normal plastids.* Plastids multiply probably by the division of pre-existing plastids only, either by constriction or by cleavage. The dividing plastids can readily be seen in the leaves of mosses and in algae.

Though there occur several distinct types of plastids, yet they are, however, really the same thing under different pigmented conditions performing different functions, for one type may turn into the other and *vice versa*. They are usually divided into *two* main categories according to functions and colour: the **leucoplasts** or transparent colourless plastids, and the **chromoplasts** or coloured plastids. Sometimes, the term **chromatophore** (colour-bearer) is used as synonymous with the chromoplast. The chromoplasts are also of *two* kinds: the green-coloured plastids are called **chloroplasts**, and the plastids coloured other than green, **chromoplasts**.

Leucoplasts (Fig. 182, H) are those plastids, which are colourless, and are found in those parts of plants, which are not exposed to sunlight, such as, underground stems, roots, *etc.* They may be

*The origin is, however, still doubted by some authorities.

spheroidal, fusiform or cylindrical in shape. When exposed to light, they usually turn green and become converted into chloroplasts. Two types of leucoplasts are recognized : small and large. The smaller types gradually develop into the larger ones, or these are converted into chloroplasts or chromoplasts, according to circumstances. The larger ones are known as **amyloplasts** (starch-builders) and their function is amyloplastic, *i.e.*, they can prepare insoluble starch grains from soluble sugar for the purpose of storage in the underground parts of plants, as in tuber, rhizome, *etc.*

Chloroplasts, the most important of all plastids, are green-coloured, owing to the presence of the green pigment, **chlorophyll**, which develops under the action of sunlight. Hence, they occur only in those parts of plants, which are exposed to sunlight. They are usually flattened and discoid, spherical or ovoid in form (Fig. 182, E). But, sometimes their forms (Fig. 182, A-D) are very unusual, and may be an irregular net (e.g., *Oedogonium*), a coiled ribbon (e.g., *Spirogyra*), a girdle (e.g., *Ulothrix*), radiating plates (e.g., *Zygnema*, Desmids), spindle-shaped (e.g., *Anthoceros*), *etc.* In some lower plants, such as algae, the chromatophores are not green, but red or brown in colour. In these cases, chlorophyll is nevertheless present, but is more or less masked by the presence of other pigments. Each chloroplast consists of a number of membranous laminations arranged in an orderly fashion forming the **grana**, and between the grana lies the **stroma**. The stroma possesses fewer or even no laminations. On the layers of the grana the chlorophyll remains spread out in monolayers.

According to Zirkle (1926), the chlorophyll, as it exists in the plastids, contains the following pigments : **chlorophyll a** (a blue-black micro-crystalline solid, $C_{55}H_{72}O_5N_4Mg$), **chlorophyll b** (a green-black micro-crystalline solid, $C_{55}H_{70}O_5N_4Mg$), **carotene** (an orange-red crystalline solid, $C_{40}H_{56}$), and **xanthophyll** (a yellow crystalline solid, $C_{40}H_{56}O_2$). Chlorophyll can be easily extracted from the green leaves by treating them with alcohol or chloroform, when, the leaves become colourless. If the green alcoholic extract is shaken with some quantity of benzene, it separates into two layers, an upper green layer of chlorophylls and the lower yellow layer of carotenoids.* The alcoholic

*Chlorophyll is more soluble in benzene than in alcohol, and benzene is lighter than alcohol.

extract of chlorophyll shows fluorescence, *i.e.*, it appears blood-red in reflected light, but deep-green in transmitted light.

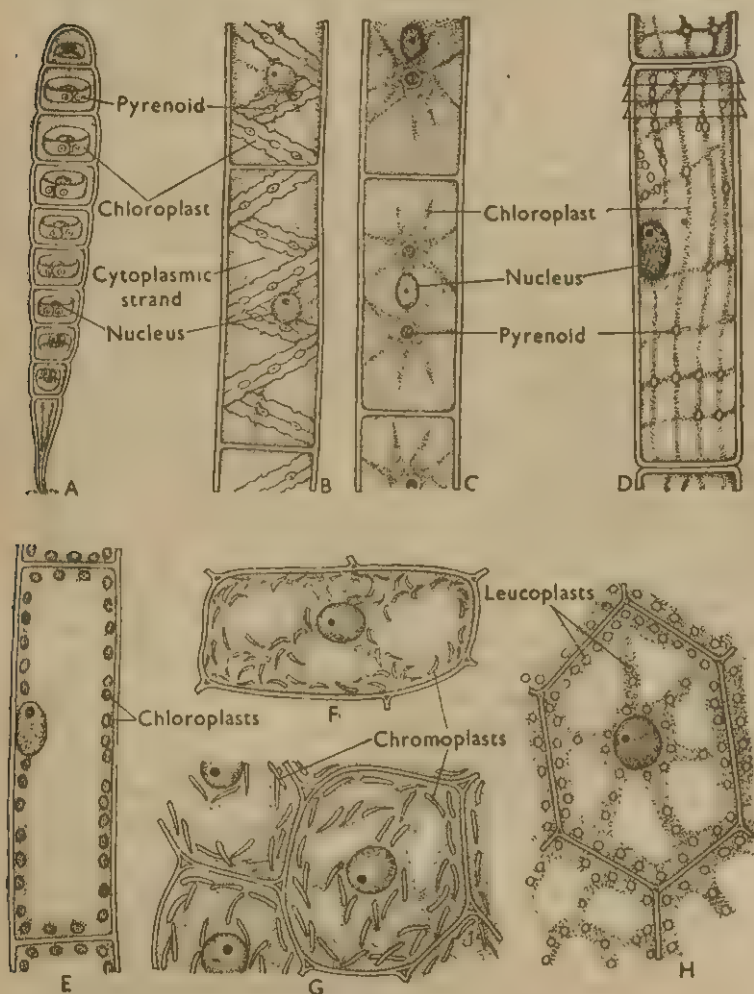


FIG. 182. DIFFERENT TYPES OF PLASTIDS

A, in *Ulothrix* ; B, in *Spirogyra* ; C, in *Zygnema* ; D, in *Oedogonium* ;
E, in *Vallisneria* ; F, in tomato ; G, in carrot , H, in maize.

In some chloroplasts, there are some peculiar structures, known as **pyrenoids**, which are highly refractive masses of proteinaceous

bodies lying within or on the chloroplasts. These are common in green and red algae, and are also found in some liverworts.

The functions of chloroplasts are *two fold* : (a) assimilatory, *i.e.*, they are capable of building up soluble carbohydrates from carbon dioxide and water in presence of sunlight, or, in other words, they are the actual photosynthetic organs of the cells (Stokes, 1864), and (b) amyloplastic or starch-building, *i.e.*, they can prepare insoluble starch grains from soluble sugars.

Chromoplasts (Fig. 182, F & G) range in colour from yellow to red due to the presence of carotenoid pigments, such as *xanthophyll* (yellow) and *carotene* (orange-red). Their shape is very variable being spherical, spindle-shaped, quite irregular, angular and even forked. Chromoplasts occur in the cells of yellow and red floral leaves and in the superficial cells of many yellow-, orange-, or red-coloured fruits. These sometimes occur in the underground roots, as in carrot, where they are in the form of irregular and somewhat pointed bodies owing to the presence of crystalline pigments within them.* The function of the chromoplasts is somewhat obscure. However, it may be said that they do not play any part in the nutritive metabolism as do the chloroplasts. They are of ecological importance, as much as bright attractive colours of petals and fruits are mostly due to them, which help in the attraction of insects and animals for effecting pollination and dispersal of fruits and seeds.

Another specialized group of plastids, called **elaioplasts**, is found to occur in the liverworts and the monocotyledons. They help in the formation of fatty substances. Faull (1935) has shown in *Iris* (Fam. Iridaceae) that these elaioplasts can form not only fatty substances but also starch.

4.5 MITOCHONDRIA

The mitochondria (which are also known as **chondriosomes**) are very small bodies ($0.2-3.0\mu$ in size), which appear in the cytoplasm in the form of minute rods, grains, spores, or filaments, and are almost universally present in all living cells. These are abundant in young active cells, and may be seen in a state of constant motion. They react positively to Janus Green and also

*Some workers like Weier (1942) challenge the validity of such bodies to be included along with the plastids.

stain with Haematoxylin. The total mitochondrial content of an organism is called the **chondriome**.

Owing to the difficulties of observation, there is much controversy regarding the origin, behaviour and biological significance of these minute objects. Under the electron microscope, however, a mitochondrion has been found to be lying enclosed by a two-layered lipo-protein memberane; the outer layer is extremely elastic, while the inner one is highly convoluted.

The mitochondria are permanent cytoplasmic organs and arise only from pre-existing ones. The older idea that they can arise *de novo* has been rejected by the modern cytologists.

Functionally, the mitochondria are the secretors of 'biological energy', and in the words of Siekevitz (1957) constitute the 'power house of the cell'. First, the mitochondria help in the liberation of energy from the carbohydrates, fats, and proteins by the process of *oxidation*. Subsequently, by another process, known as *phosphorylation*, this energy is stored up in other phosphate (PO_4)—containing molecules, the principal one of which is adenosine triphosphate (ATP). The mitochondria then secrete this ATP, which is utilized by any part of the cell wherever there is a need for energy.

GOLGI BODIES

The golgi bodies (also known as **lipochondria**), according to their discoverer Golgi, are peculiar to animal cells; but similar structures were also demonstrated in a few plant cells, *e.g.*, in the root tips of *Allium* and *Lilium* of Fam. Liliaceae, *Iris* (Fam. Iridaceae), *etc.*, by special methods of preparation. They are rich in fatty materials and usually form more or less extensive networks in the cytoplasm. Though their biological significance is not yet properly understood, yet, as they are specially noted within secretory cells, it is presumed that they probably play an important part in secretion.

CENTROSOMES

The centrosomes are characteristics of animal cells, but are also found in some lower plants, *e.g.*, *Dictyota*, *Fucus*, ascomycetous fungi, *etc.* Each centrosome typically consists of a central granule, called the **centriole**, which is embedded in a hyaline

matrix, the **centrosphere**. At the time of nuclear division, each centrosome becomes surrounded by conspicuous radiating rays, known as the **astral rays**, and is often divided into two. They appear to be concerned with the orientation of the prophasic karyolymph to form the spindle.

VACUOLES

When the cell grows, the growth of the cytoplasm cannot keep pace with the growth of the cell wall, hence, numerous cavities, known as **vacuoles** or **sap cavities** are formed within the cytoplasm. Recent researches, however, show that vacuoles are permanent constituents of a cell, and play an important role in the metabolism (Guilliermond ; Dangerad). The presence of

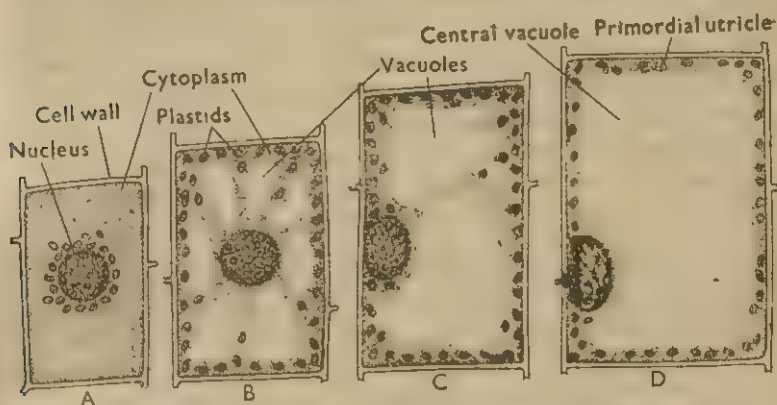


FIG. 183. STAGES IN THE DEVELOPMENT OF A CELL SHOWING THE FORMATION OF THE PRIMORDIAL UTRICLE.

numerous small vacuoles in the apical meristems of vascular plants has been demonstrated by Zirkle, and they may exhibit a variety of forms (Bailey). The vacuolar system in the protoplast containing one or more vacuoles is known as the **vacuome** (Dangeard). As the size of the cell increases, the vacuoles also increase in number, enlarge, and ultimately run together forming a single big vacuole, which occupies the centre of the cell. The cytoplasm then forms a thin lining layer round the inner surface of the cell wall, and is known as the **primordial utricle** (Fig. 183). These vacuoles are not empty spaces, but are filled up with a watery ergastic fluid, the **cell sap**.

The cell sap is not pure water. Various chemical substances are found present in it, either in solution or in colloidal states. The cell sap gives an acid, neutral, or alkaline reaction depending on its constituents. The chief constituents of the cell sap are : *organic acids*—malic acid, oxalic acid, *etc.*, and their salts ; *reserve materials* (i.e., substances to be used up in the growth process), which include mainly (a) carbohydrates (various sugars, such as, cane sugar, grape sugar, inulin, *etc.*, occurring in solution), and (b) proteins ; *inorganic salts*, such as, nitrates, sulphates, phosphates, *etc.*, *excretory products*, such as, alkaloids, tannins and glucosides ; and *plant pigments*. The cell sap is often coloured by the presence of a pigment, known as **anthocyanin**. It forms red solution in an acid cell sap and blue in an alkaline one. It gives bright coloration to many flowers and fruits, and thus helps to attract insects and animals for pollination or dispersal of fruits and seeds. In young organs it also acts as a light-screen preventing excessive illumination. Sometimes, a yellow-colouring matter, known as **xanthene**, is also found. It is soluble in water and is related to xanthophyll. The cell sap may sometimes contain alcohols, enzymes and also solid or fluid particles of oils, tannins, gums, starch, *etc.*, in a state of suspension.

The different vacuoles of the same protoplast may not have the same contents. Thus, one vacuole possessing coloured cell sap may occur side by side with others having colourless cell sap. A vacuole may contain tannin, but the neighbouring one may be entirely devoid of that substance. Besides the vacuoles containing a watery cell sap, there are others, known as **oil vacuoles**, which are similar to the water vacuoles, but contain droplets of oil and never attain a large size.

Functionally, the cell sap saturates the cell wall and protoplasm, and contains various kinds of reserve materials and osmotic substances, by means of which water is absorbed, thus making the cell turgid. In course of the metabolic activities of protoplasm, various poisonous substances are formed, and these are stored up in the cell sap. Thus, the plants are saved from their poisonous effects. The presence of various colouring matters in the cell sap of many flowers and fruits helps to attract insects and animals for pollination and dispersal of fruits and seeds.

ERGASTIC SUBSTANCES

The ergastic substances are the non-living protoplasmic inclusions found chiefly in the cytoplasm and vacuoles, either in a dissolved state or as visible crystals, droplets or granules. These include various reserve materials, as well as secretory and excretory products of metabolism.

RESERVE MATERIALS

These substances are constructed by the protoplasm during nutrition, and are stored up in special cells for the future use of plants ; thus, they constitute the foods of plants. They exist either in the solid or in the liquid state, and they may be either nitrogenous or non-nitrogenous. The non-nitrogenous substances are carbohydrates, fats and oils, while the nitrogenous ones are the various types of proteins.

A. Non-nitrogenous Reserve Materials

(a) CARBOHYDRATES

Carbohydrates are those substances, which consist of carbon, hydrogen, and oxygen, the latter two being present in the same proportion as they do in water. When heated, water escapes from a carbohydrate, and it becomes charred forming a black mass of carbon. Some carbohydrates are insoluble in water, while others are soluble. The insoluble ones are starch grains, cellulose, and glycogen, while the soluble ones are sugars and inulin.

Starch grains. Starch is an insoluble carbohydrate. It is an important plant food. Its chemical formula is $(C_6H_{10}O_5)_n$. Starch occurs in the form of minute grains in almost all parts of the plant body, and these are termed as **starch grains**. They are stored up in large quantities in the fleshy roots and underground stems. They are abundantly found in the pith of sago palm (*Metroxylon rumphii* of Fam. Palmae). The cereals, like rice, maize, wheat, etc., contain abundant starch grains. Most starch grains contain a substance, known as **amylose**, which turns blue when treated with dilute iodine solution. They also

contain a mucilaginous substance, called **amylopectin**, which is responsible for the pasty union of the starch grains, when treated with boiling water and alkalis. They are insoluble in cold water, alcohol and ether.

Starch grains are of *two* kinds : **assimilation starch** and **reserve starch** or **storage starch**. The assimilation starch grains are manufactured in the leaves by the chloroplasts during photosynthesis, and are temporarily stored up in them. Reserve starch grains are somewhat bigger in size and have definite shapes. They are chiefly manufactured by the leucoplasts, and also by the chloroplasts, from the sugar solution in the absence of light, and are usually stored up in the storage tissues. Starch grains, whether formed by the leucoplasts or by the chloroplasts, are always produced within the body of the plastids, but what happens exactly at maturity is not yet properly known. Starch grains are insoluble, but, when required for nourishment, they are converted into soluble forms (sugars) by the action of an enzyme, known as **diastase** or **amylase**.

When a reserve starch grain is observed under the microscope, it exhibits a stratified appearance. (Fig. 184). This stratification

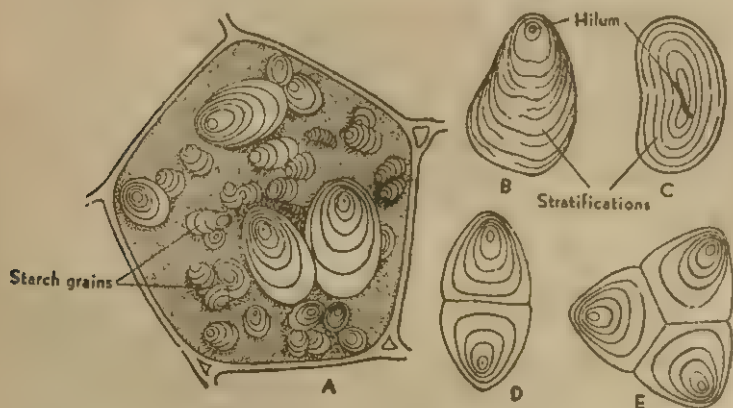


FIG. 184. STARCH GRAINS

A, starch grains in a cell of the potato tuber ; B, simple and eccentric ;
C, simple and centric ; D, semi-compound ; E, compound.

is due to the presence of alternate layers of starch substance containing varying amount of water, and thus differing in their

densities (Frey-Wyssling, 1948). These layers are laid down one after another due to the diurnal periodicity in the activities of the plastids forming them (Esau, 1953) around a definite spot, known as the **hilum**, which represents the first-formed portion of the grain. The hilum is highly refractive to light and may be rounded, angular, stellate, lobed or sometimes forked. When the hilum is situated at one end of the grain, it is called **acentric** or **eccentric**, as in potato (*Solanum tuberosum* of Fam. Solanaceae); but when centrally placed, it is called **centric**, as in pea (*Pisum sativum* of Fam. Leguminosae). When the starch grains are quite separate from one another, they are said to be **simple**; simple starch grains are very common. But, sometimes two or more grains are compressed together to form a **compound** starch grain. If a compound grain is enveloped by a few common layers of starch material, it is then said to be **semi-compound**. Starch grains are of various forms in different plants. Thus, in potato they are more or less oval, in pea slightly irregular, in rice and maize polygonal, in the latex of *Opuntia* dumb-bell-shaped, and so on.

According to the theory developed and elaborated by Nageli, Schimper, and A. Meyer, the starch grain is a crystalline sphaero-crystal with radially arranged needle-shaped crystals (**trichites**) differing in their length, thickness, closeness and branching in different layers.

Tests: (1) Starch grains turn blue to black with iodine solution depending on its concentration. (2) They also turn deep-blue with chlorzinc-iodine solution (Schultze's solution), but gradually lose their brightness.

Reserve cellulose. Cellulose is a solid carbohydrate substance. It occurs as an extra layer of thick cellulose wall in the endosperm of some seeds, such as date (*Phoenix sylvestris*) and coconut (*Cocos nucifera*), both belonging to Fam. Palmae. When required for nutrition, it is converted into sugar by the action of an enzyme, called **cellulase**.

Glycogen. Glycogen (also known as **animal starch**) is a carbohydrate substance like starch, and is found chiefly in the fungi. It also occurs in some algae. It is usually distributed in the cytoplasm as an amorphous body in the interior of the fungal hyphae. Glycogen fulfils the same requirement in fungi as starch

and sugars do in the higher plants. It is converted into sugar by the action of an enzyme, known as **glycogenase**.

Test : Glycogen turns reddish-brown with iodine solution.

Sugars. Sugars are soluble carbohydrate substances. Different kinds of sugars are present in the plants. Grape sugar, ($C_6H_{12}O_6$), the simplest form of carbohydrate is found in the ripe fruits and in the fleshy underground leaf-bases of onion (*Allium cepa* of Fam. Liliaceae) and allied plants. Cane sugar, ($C_{12}H_{22}O_{11}$), is present in large quantities in the roots of beet (*Beta vulgaris* of Fam. Chenopodiaceae) and in the stems of sugar-cane (*Saccharum officinarum* of Fam. Gramineae). When required for nutrition, the different kinds of sugars are converted into grape sugar by the action of enzymes.

Tests : Section containing grape sugar, when placed in a solution of copper sulphate, washed and heated to boiling in caustic potash solution, gives a brick-red precipitate of cuprous oxide. If cane sugar is present, the same treatment gives a blue coloration.

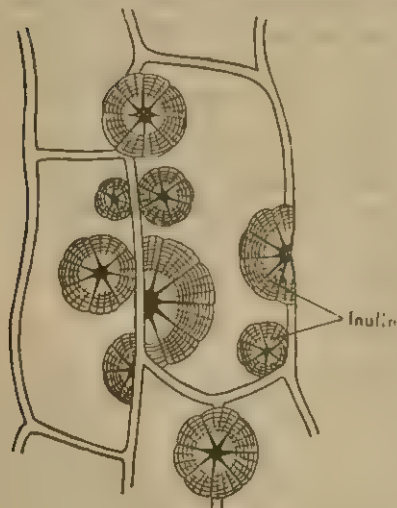


FIG. 185. INULIN CRYSTALS IN THE CELLS OF *Dahlia* TUBER.

Inulin. Inulin, ($C_6H_{10}O_5$)_n, is a kind of soluble carbohydrate, which is found in the cell sap of the roots of *Dahlia* (Fig. 185), Jerusalem artichoke (*Helianthus tuberosus*) of Fam. Compositae, etc. When treated with 95% alcohol or dilute glycerine for a considerable time, inulin precipitates out in the

form of fan-shaped crystals at the corners or across the cell walls.

(b) FATS AND OILS

Fats and oils are compounds (esters) of fatty acids and glycerols, and are fixed or non-volatile. Like carbohydrates,

these also contain carbon, hydrogen, and oxygen, but the latter two elements are not present in the same proportions, as they do in water. The oxygen contents in these cases are much less, while the proportions of carbon and hydrogen are higher than in the carbohydrates. They also constitute important plant foods. They are particularly abundant in those seeds, which are deficient in carbohydrates, and usually occur in the form of droplets in the general mass of cytoplasm. In the epidermal cells of Orchidaceae and Liliaceae, there occur special structures, known as **etioplasts**, containing cytoplasm with drops of oil. It is believed that these are formed from carbohydrates and are used up during respiration, producing energy in plants. At ordinary temperature, fats are solids, while oils are liquids. A fixed oil always leaves a permanent grease spot or a translucent mark on a piece of paper.

Tests: (1) Fats and oils stain red with Sudan III. (2) They turn brown to black with osmic acid (1% solution in water). (3) They are insoluble in water and alcohol (except castor oil and croton oil, which are soluble in higher grades of alcohol), but readily soluble in ether, petroleum and chloroform.

B. Nitrogenous Reserve Materials

The nitrogenous reserve materials always contain some amount of nitrogen in addition to carbon, hydrogen, and oxygen; in some cases, they also contain sulphur and phosphorus. These substances occur either in solid or in liquid states, and are present in every living cell. The nitrogenous reserve materials can only be translocated (from cell-to-cell) to the different parts of the plant body only in the liquid state.

PROTEINS

Proteins are the most complex as well as the most important insoluble nitrogenous reserve materials found in plants. Being reserve materials, these are classed as plant foods, and form an essential constituent of the protoplasm, and hence, are present in every living cell. The nucleus is particularly rich in the protein substance, known as **nucleoprotein**. Proteins are formed in the vacuoles rich in albumen, and gradually harden into grains, usually in the form of crystals. They are found abundantly in the storage

regions and particularly in the seeds, which are normally rich in oil or deficient in carbohydrates. Proteins may be amorphous or crystalline. The former occur in shapeless masses or globules, and the latter are generally known as **crystalloids**. When the crystal-

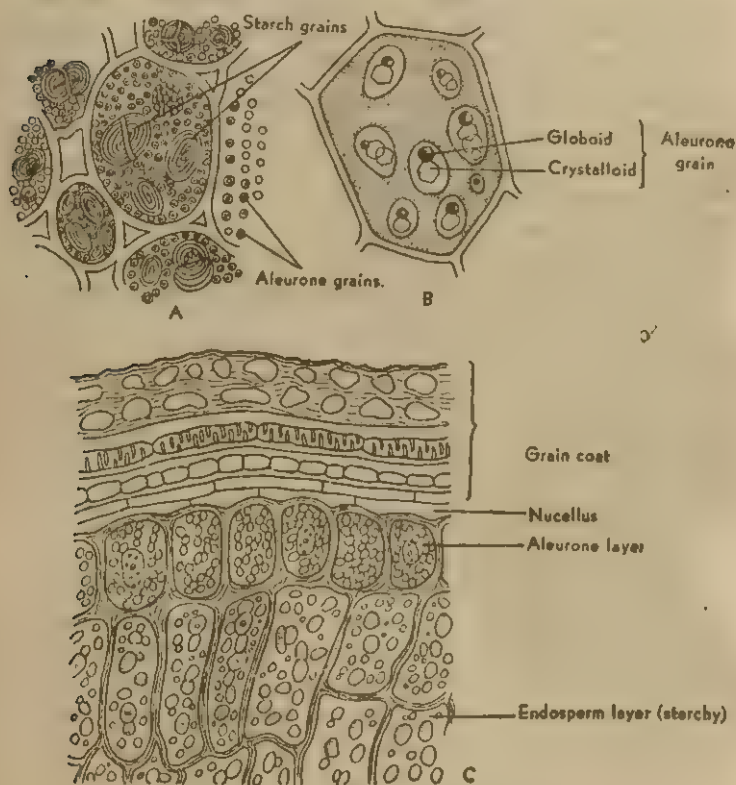


FIG. 186. ALEURONE GRAINS

A, of pea ; B, of castor seed ; C, of wheat grain.

loids combine with the amorphous proteins, they form the **aleurone grains**, which are found in the embryo, the endosperm, and the perisperm of a number of seeds. These are abundant in the cells of the cotyledons of pea (*Pisum sativum* of Fam. Leguminosae, Fig. 186, A). In cereals, such as maize wheat, oat, etc., they are localized in a layer of cells, lying next to the grain coat (Fig. 186, C). In the endosperm of castor (*Ricinus communis* of Fam. Euphorbiaceae), associated with the crystalloid, there is a more or

less clear and globular mineral matter, known as the **globoid** (Fig. 186, B), which is a double phosphate of calcium and magnesium. -

SECRETORY PRODUCTS

The secretory products are formed during the metabolic activities of the protoplasm. These substances are not concerned in the nutrition of plants, but are of some use to them. The secretory products include plant pigments, enzymes, and nectar.

PLANT PIGMENTS

Various pigments are found in plants, and these impart bright colours to flowers, fruits, *etc.* **Chlorophyll**, which is associated with plastids, is one of the most important colouring matters of plants ; it is absolutely necessary for photosynthesis. **Anthocyanin**, which is another important colouring matter, is usually found dissolved in the cell sap, but in some cases, it occurs in the form of crystals. It can be extracted with water, alcohol, and ether. The colour of the anthocyanin is dependent upon the reaction of the sap with which it is associated. Thus, when the sap is acid in reaction, it is red, but when alkaline, it is blue. It occurs in flowers, young coloured stems, roots (*e.g.*, beet root), young red leaves (*e.g.*, mango, country almond, *etc.*), and generally masks the chlorophyll. In young organs, it may have a screening effect against too strong a light. Besides these, there are **carotenoids**, carotene and xanthophyll, which occur either in association with chlorophyll or independently in the plastids (chromoplastids), and are never found dissolved in the cell sap. The function of the colouring matters in flowers is to attract the insects to bring about pollination, and in fruits to effect dispersal of seeds. Some useful dyes, like indigo, are obtained from the plant *Indigofera tinctoria* of S.F. Papilionaceae of Fam. Leguminosae.

ENZYMES

Enzymes or ferments, the peculiar nitrogenous substances which are secreted by the protoplasm, act as organic catalysts. They are always associated with living cells, and play an important part in the various life-processes of plants, *viz.*, respiration,

assimilation, digestion, *etc.* They have the power to convert the insoluble foods into soluble and diffusible forms without themselves being used up in the process (for a fuller account *vide* section on Plant Physiology, Vol. II).

NECTAR

The nectar is a sweet-tasting, sugar-containing fluid, secreted by some glandular surfaces or specialized structures, which are developed directly on the receptacle. These bodies are known as the **nectar glands** or **nectaries**. The nectaries occur in various parts of the flower. The nectar-secreting tissue may be composed of purely epidermal cells, or of epidermal cells associated with some sub-epidermal ones. The nectar is meant for the attraction of insects to bring about pollination.

EXCRETORY OR WASTE PRODUCTS

These are by-products of metabolism, and are of no use to the plants from the nutritive point of view, but have considerable economical importance. As plants, like animals, have no special excretory organs, these are generally packed up in certain cells of plants, usually far away from the seat of protoplasmic activity. The various waste products are the organic acids, alkaloids, gums, resins, tannins, etherial or essential oils, latex, and mineral crystals.

ORGANIC ACIDS

Different kinds of organic acids are found in the cell sap of many plants. Thus, **citric acid** is found in lemon, **tartaric acid** in tamarind, **oxalic acid** in wood sorrel, **malic acid** in apple, and so on. The function of the organic acids is mainly physiological, and these are particularly useful during respiration.

ALKALOIDS

Alkaloids are complex nitrogenous substances composed of carbon, hydrogen, oxygen, and nitrogen. These occur in association with some organic acids in various parts of plants, specially roots, seeds, leaves, barks, *etc.* Most of these are poisonous, bitter in taste, and occur both in crystalline and liquid forms, being readily soluble in alcohol. Some of the best known

alkaloids are the **quinine**, present in the bark of *Cinchona* tree, **nicotine** in the leaves of tobacco, **morphine** in opium poppy, **strychnine** in the seeds of *nux vomica*, **cocaine** in the leaves of coco, **thein** in the leaves of tea, and **caffein** in coffee.

GUMS

Gums are products of decomposition of the cellulose cell wall. Camphor, balsams, gum arabic of commerce, *etc.*, are familiar examples.

RESINS

Resins are solid, brittle, non-volatile, complex substances, which are derived from the oxidation of volatile oils. They are soluble in alkalies (forming **resin-soaps**) and alcohol, but insoluble in water. When they remain soluble in volatile oils, these are known as **oleo-resins**, *e.g.*, copaiba, canada turpentine, *etc.* Sometimes, they are found in combination with gums and volatile oils, and are then known as **gum-resins**, *e.g.*, asafoetida. They form emulsion when mixed with water.

TANNINS

Tanniferous bodies are nitrogenous substances, which occur widely in plants in the form of minute granular or round particles, or in fused masses, particularly in the cytoplasm of the cells of cortex and phloem. They are chiefly found in parenchyma cells, but may also be noted in collenchyma and cork cells. Sometimes, they are found dissolved in protoplasts forming gummy or mucilagenous masses. Tannins are chiefly found in the phloem of oak (*Quercus* sp. of Fam. Cupuliferae), in the fruits of tamarind (*Tamarindus indicus* of S.F. Caesalpinieae), and myrobolan (*Terminalia chebula* of Fam. Combretaceae), *etc.* **Catechu**, a kind of tannin, is extracted from *Acacia catechu* of S.F. Mimosae (Fam. Leguminosae). The presence of tannin in the wood increases its durability, and thus enhances its value. Tannins are regarded as substances (a) guarding the cell against desiccation, decay or injury, (b) associated in some way to starch metabolism, as well as formation and transport of sugar, and (c) as protective colloids of the cytoplasm (Hauser, 1935).

Tests : (1) Tannins turn dark blue or green, when treated with ferric chloride or ferrous sulphate solution. (2) When they are treated with an aqueous solution of potassium bichromate, a reddish-brown precipitate is obtained.

ETHERIAL OR ESSENTIAL OILS

These are volatile oils, which are chiefly found in flowers and fruits. They readily volatilize, when exposed to air, and have characteristic odours. Common examples of volatile oils are lemon oil, oil of winter green, oil of peppermint, *etc.* These mostly occur in **oil glands**, as in the leaves of lemon (*Citrus limon* of Fam. Rutaceae), *Eucalyptus* sp. of Fam. Myrtaceae, *etc.*, and in the rind of orange (*Citrus sinensis*=*C. aurantium*), shaddock (*Citrus grandis*=*C. decumana*), both of Fam. Rutaceae, *etc.* Their composition is very variable from that of fixed oils, and these are never used as food. Volatile oils, unlike fixed oils, never leave any stain on a piece of paper. The odour of flowers often helps in the process of pollination by inviting the insects. The repulsive odour often protects the plants from the attacks of herbivorous animals.

Tests : (1) Etherial oils turn pink with alkanet. (2) They are soluble in 90% alcohol.

LATEX

The latex is an emulsion consisting of a matrix of watery fluid in which various substances, such as starch grains, sugars, proteins, enzymes, alkaloids, *etc.*, remain suspended or dissolved. It is secreted by a cell or a vessel in which it is contained, and is conducted through it to the different parts of the plant body. Usually, it is milk-white in appearance. This milky appearance is due to the presence of minute globules of coutchouc and gutta-percha, and are found in the families of Euphorbiaceae, Moraceae, Zapotaceae, Apocynaceae, Asclepiadaceae, *etc.* In some cases, the latex is poisonous, for which plants possessing latex are disliked by animals. The latex of *Hevea*, *Ficus*, *etc.*, is the source of rubber. From the latex of papaw (*Carica papaya* of Fam. Caricaceae) a digestive substance, known as **papaine**, is extracted. The latex is of some use to the plant in the healing of wounds. When any part of the plant body is wounded, the latex comes out and afterwards forms a clot, thus healing up the wound, and

hence, prevents the entrance of fungi or bacteria through the wounded parts.

MINERAL CRYSTALS

Mineral crystals occur in all parts of plants, particularly water plants and monocotyledons, and are specially abundant in the pith, cortex and phloem. Crystals lie either in the protoplasts or in the lumens of dead cells, *e.g.*, in fibres. Usually, there is one type of crystal in each cell, but in some cases, two or more types occur together. Mineral crystals are found either as siliceous bodies in the cytoplasm of the cells of palms and orchids and often completely filling them, or as crystals of calcium oxalate, which are stored up in the cells of different parts of the plant body. Calcium oxalate crystals occur in various forms: (1) as rods, prisms, cubes, octahedra, *etc.*, in the tunic of onion (*Allium cepa* of Fam. Liliaceae, Fig. 187), (2) as bunch of needle-shaped crystals, known as **acicular raphides** (Fig. 188, A), in special mucilagenous parenchyma cells of the petioles of arum (*Colocasia antiquorum* of Fam. Araceae), water hyacinth (*Eichhornia speciosa* of Fam. Pontederiaceae), the leaf-bases of *Pistia*, and in underground stems of arum, *Amorphophallus*, *etc.*, all of Fam. Araceae, (3) as rounded or more or less crystalline star-like aggregates, called **conglomerates** or **sphaeraphides** (Fig. 188, B), in special mucilagenous parenchyma cells of the petioles of water hyacinth and of the leaf-bases of *Pistia*, *etc.* These

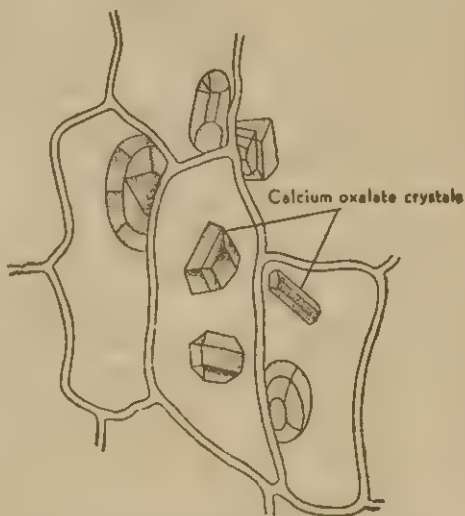


FIG. 187. CALCIUM OXALATE CRYSTALS FROM THE TUNIC OF ONION.

special cells containing the raphides usually project into the air spaces of the organs.

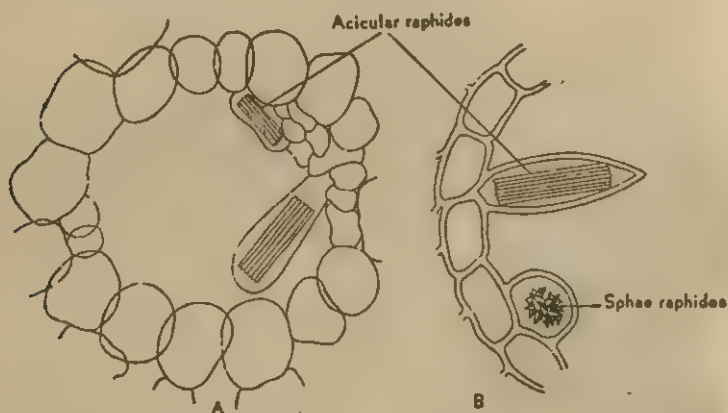


FIG. 188. RAPHIDES

A, from the petiole of *Colocasia* ; B, from the leaf-base of *Pistia*.

Tests : (1) Raphides dissolve in mineral acids without evolution of any gas. (2) They are insoluble in weak acetic acid.

CHAPTER II

THE CELL WALL

The presence of the cell wall is a characteristic feature of plant cells. With very few exceptions, as in the zoospores of algae and fungi, or the gametes of all categories of plants, a cell is always provided with a thin and delicate membrane, the **cell wall**, enclosing the protoplast. Generally, the animal cell does not possess any such wall. The cell wall is usually considered as a non-protoplasmic structure, whose formation and development are regulated by the protoplasm itself. Some recent workers, like Heyn (1940) and Frey-Wyssling (1950), however, regard it as a living structure, which is capable of regulating its own growth. The cell wall is easily permeated by water and gases in solution, and holds water in its body. It protects the protoplasm from external danger, preserves the form of the cell, and gives strength to it.

The cell wall is made up of a substance, called **cellulose** of the carbohydrate group, having the chemical formula $(C_6H_{10}O_5)_n$. The primary wall, when first formed, is made up of a carbohydrate, called **pectose**, until it attains the full size, and becomes firm and hard due to the formation of insoluble pectates, like calcium pectate. On the primary wall the secondary walls, which are made up of pectose and cellulose, are laid down. But the tertiary layers, which are deposited later, are entirely made of cellulose. Soon these inner layers are transformed into mucilage. In extreme cases, however, the primary wall is also partly affected.

CELLULOSE is present in the walls of all cells of plants, excepting the majority of the fungi. It is permeable to water and gases in solution. Cellulose turns blue to violet with chlor-zinc-iodine. It is not soluble in water, alcohol, alkalies or dilute acids, but dissolves in a fresh solution of cuprammonia (cupric oxide in strong ammonia).

PECTIC SUBSTANCES are particularly prominent in non-lignified cells. These stain more deeply with safranin and methylene blue, hence, pectin-cellulose and cellulose can be easily differentiated.

CALLOSE is always present in calcified cell-wall layers in cells containing cystoliths. It also envelops the sieve plates. It is coloured reddish-brown by chlor-zinc-iodine, and becomes intense blue with aniline blue. It is insoluble in cuprammonia.

CHITIN is present in the cell walls of fungi, and takes the same place as cellulose in the cell walls of higher plants.

MIDDLE LAMELLA (Fig. 189). The middle lamella, whose presence can only be demonstrated by means of special techniques, is an amorphous colloidal substance, made up of mainly calcium and magnesium pectates. Esau (1953), following Kerr and Bailey (1934), considers only the intercellular substance as the middle lamella. Other workers, however, regard the two primary walls of adjacent cells along with the intercellular substance as one unit. This unit, which is strongly lignified, is also referred to as the middle lamella. In some cases, the intercellular substance may be obscure, when the middle lamella is termed as a **compound** one. The middle lamella often shows thickening at the corners between the cells.

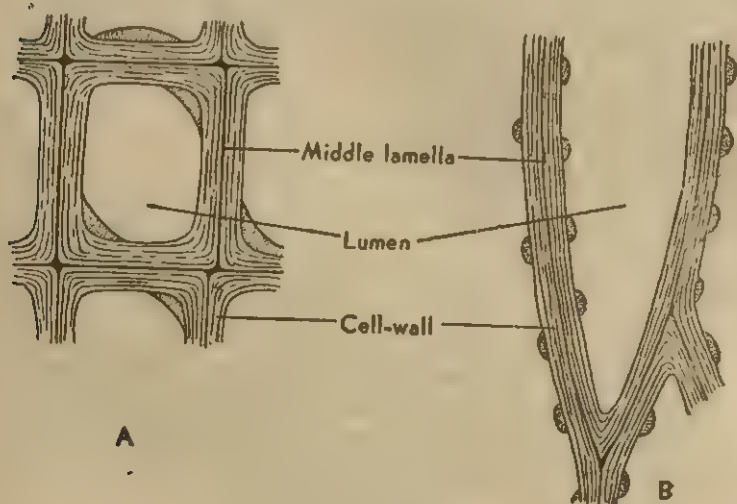


FIG. 189. MIDDLE LAMELLA

A. in t.s. ; B. in l.s.

PLASMODESMATA (Fig. 190). In the early stages of wall formation, the fluid cell plate as well as the mesh-like primary

walls are partly cytoplasmic in nature. As the layers become strengthened by cellulose and pectic materials, cytoplasmic connections persist as slender threads or strands, thus establishing direct connections between the adjacent protoplasts. These delicate strands are known as **plasmodesmata**. Owing to extreme fineness, these strands are not usually seen unless suitably stained. Workers like Schumacher (1942), and Livingston and Bailey (1946) are doubtful about the continuity of the plasmodesmata from one cell to another, whereas there are others, who even deny their cytoplasmic nature, and consider them as mere artifacts, developed during the treatment of the cells. The demonstration

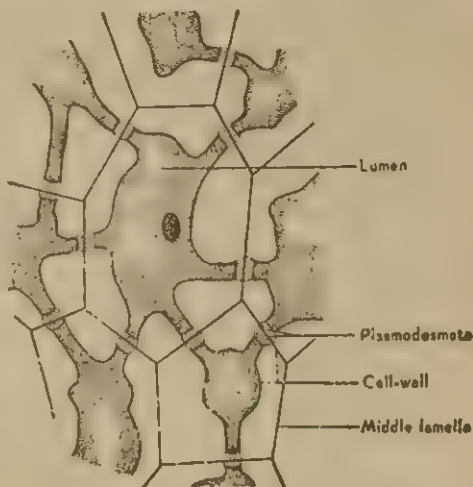


FIG. 190. PLASMODESMATA IN THE ENDOSPERM OF DATE
(Redrawn from Holman & Robbins).

of the presence of the plasmodesmata in the living cells of the cambium as well as the ray cells of some gymnosperms, however, provides a very strong support to their cytoplasmic nature. They are found to be present in the Rhodophyceae among algae, Hepaticae and Musci among the bryophytes, as well as in the different groups of vascular plants. The probable functions of the plasmodesmata are twofold : they are regarded as channels for translocation of food, as well as for the conduction of stimuli.

ORIGIN AND DEVELOPMENT OF THE CELL WALL

The cell wall, as stated before, is formed by the vital activity of the protoplasm. But, the question arises as to the exact method in which it is formed. According to some botanists, the cell wall is secreted by the protoplasm in the form of a

membrane. But, according to others, the cell wall is formed by the actual conversion of the peripheral layer of protoplasm into the cell-wall substances. Recent researches, however, tend to support the view that the cell wall, in general, is a secretion product.

When a young cell gradually increases in dimension, its cell wall also increases in surface area and remains thin. But, when it attains its ultimate size, the growth in thickness of the cell wall begins. Thus, the cell wall grows in two directions, *viz.*, in surface area and in thickness.

Growth in surface area. When a cell grows in size, the cell wall is stretched. In order that the cell wall may be continually stretched, fresh particles of cell-wall substance are added or thrown into the interior of the old membrane, and these are ultimately intercalated, or pushed in, between the particles of the old cell-wall substance. In this way, the cell wall grows in surface area. This process of growth was termed as **growth by intussusception** by Nageli.

Growth in thickness. There are two methods by which a cell wall may increase in thickness and these are : by **apposition**, *i.e.*, when new particles of cell-wall substance are deposited separately and successively upon the old inner surface of the cell wall, where these become ultimately incorporated in the framework of the wall ; and by **superposition**, *i.e.*, when the thickening takes place not by the deposition of separate particles, but by the laying down of entire fresh layers or lamellae of new cell-wall substance on the inner surface of the old one, and superimposed or placed one upon the other like the leaves of a book. This view is supported by Strasburger and others. Haberlandt and others consider it as a variety of apposition.

The thickening of the cell wall is either **centrifugal**, *i.e.*, away from the centre, or **centripetal**, *i.e.*, towards the centre. Centrifugal development takes place on the free surfaces of certain cells, such as spores, pollen grains, epidermal cells, *etc.* Centripetal development renders the cell wall thick in most cases.

GROSS LAYERS OF THE CELL WALL (Fig. 191).

According to origin, as well as chemical and physical natures, there are *three* main categories of wall layers. These are *intercellu-*

lar layer, the *primary wall*, and the *secondary wall*. Of these, the first one (the *intercellular layer*) is derived from the cell plate (following mitosis), which may be more or less lignified in xylem elements. The *primary wall* is composed largely of

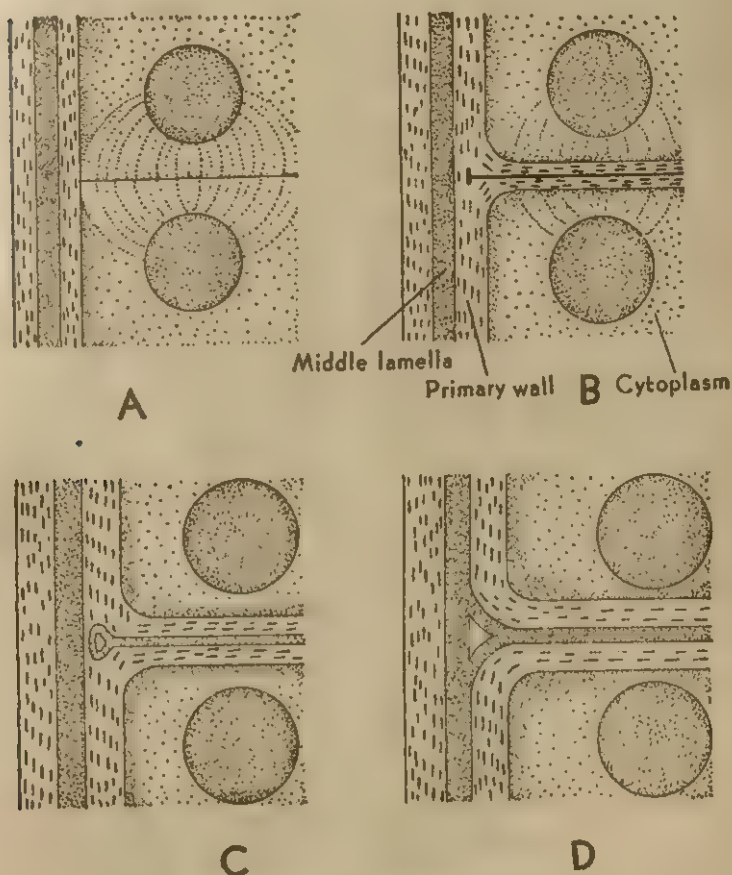


FIG. 191. STAGES IN THE DEVELOPMENT OF GROSS LAYERS OF THE CELL WALL
(Modified after Eames & MacDaniels).

cellulose, which is secreted on both sides of the cell plate; it is provided with plasmodesmata and is capable of re-adjustment during tissue development. The *secondary wall*, a physically and chemically complex substance, is generally formed after a

cell has attained its final shape and size. This layer is usually incapable of undergoing reversible changes in thickness ; it is commonly found in tracheids and fibres, showing stratifications in the wall. The secondary layer is rarely a continuous one and often develops as rings, spirals, a complex network or in the form of pits.

THICKENING OF THE CELL WALL

Usually, growth in thickness of the cell wall does not take place till the cells have attained their full size. The thickening

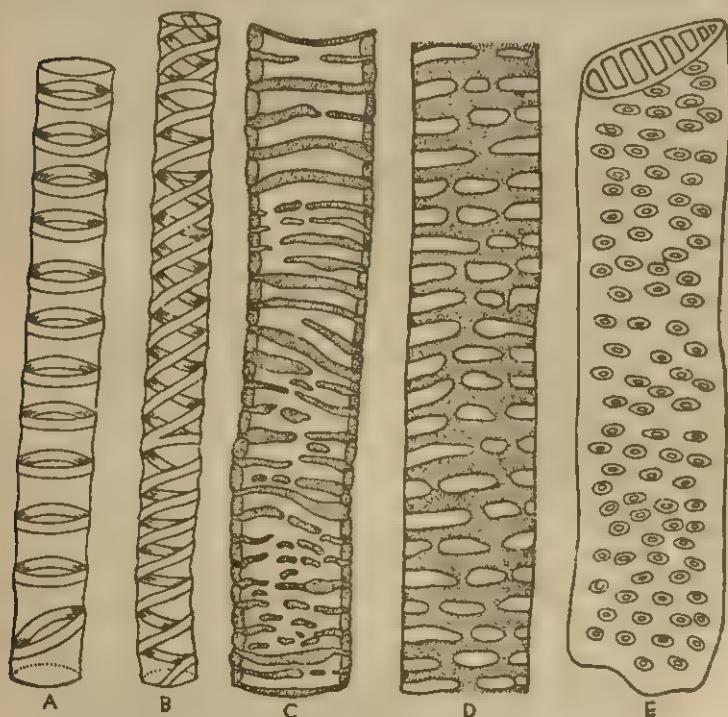


FIG. 192. DIFFERENT TYPES OF THICKENING OF THE CELL WALL
A, annular ; B, spiral ; C, scalariform ; D, reticulate ; E, pitted.

of the cell wall is mainly due to the deposition of lignin or cellulose. Generally, thickening does not take place uniformly all round the cell wall, but most commonly it is localized, *i.e.*, some parts become thick, while others remain thin, so that the water containing various mineral matters in solution may pass in and out

of the cell. When the walls become thickened, the cells gradually lose their protoplasmic contents, and become dead. The thickenings give rigidity to the cell wall, and enable it to withstand external pressure.

The localized thickenings result in the formation of various patterns or markings on the inner cell walls (Fig. 192) as follows : when thickenings take place in the form of rings, **annular** ; in the form of spiral bands, **spiral** ; like the steps of a ladder, **scalariform*** ; in the form of a network, **reticulate** ; and **pitted**, when thickenings take place, more or less uniformly, the cell wall leaving numerous unthickened circumscribed areas, which appear like so many perforations, apertures or slits, and such

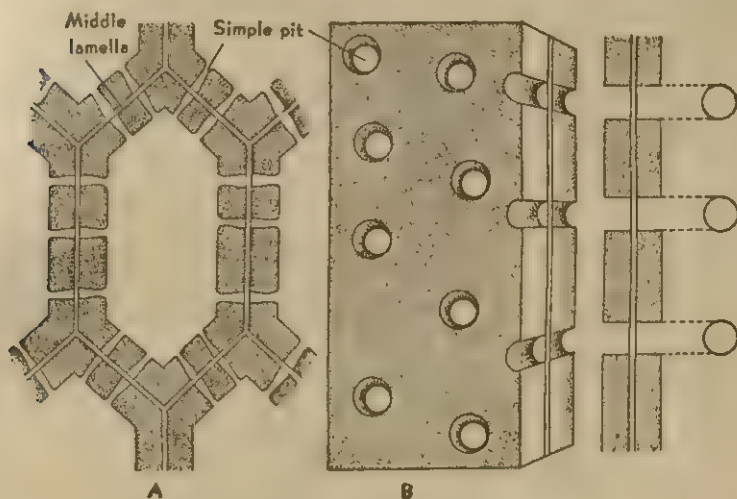


FIG. 193. SIMPLE PITS IN DIFFERENT VIEWS
(Redrawn from Holman & Robbins).

unthickened apertures are known as **pits**. The pits vary in size, shape and number. They are found in all types of cells, excepting a few thin-walled ones, and become minute and scarce in some types of fibre. Through these pits interchange of materials takes place between the cells. Pits usually occur in pairs, *i.e.*, a thin area on the secondary wall lies opposite to a similar area

*Cells with scalariform thickening are characteristically found in the xylem of the pteridophytes.

of the adjacent cell forming a **pit-pair**. In some cases, a solitary pit is developed on one side of the wall only without having any corresponding pit on the adjacent wall. This type of pit is known as a **blind pit**. A **simple pit-pair** consists of the **pit cavity**, i.e., the actual space within the secondary wall, the **pit aperture** or opening into the cavity, separated by a **pit membrane** (or **closing membrane**), which represents the common wall composed of the intercellular substance and the primary walls. Pit-pairs arise in young cells on the primary **pit-fields**, which are nothing but thinner areas of the intercellular layer and primary walls. The pits may be either **simple**, or **bordered**.

Simple pits (Fig. 193) are well developed in vessels, fibres, xylem parenchyma, as well as in ordinary parenchyma. They appear as circular or oval areas in surface view, and the cavities have equal diameters throughout, without any over-arching rim or border of the secondary wall in sectional view.

Bordered pits (Fig. 194), are mainly typical of tracheids of gymnosperms, but may also be found in the vessels of some

angiosperms, like *Acer*, *Magnolia*, *Drimys*, etc. They are really simple pits provided with a border or a rim. A part of the cavity of each pit is over-arched by a rim-like development of the secondary wall, known as the **pit border**, and the part, thus enclosed, is called the **pit chamber**. The

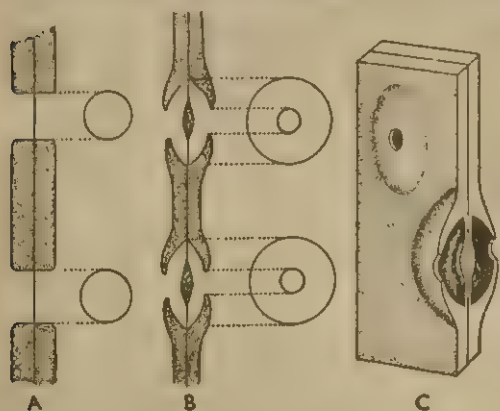


FIG. 194. BORDERED PITS

A, surface view ; B, side view ; C, perspective view.

opening in the pit border is termed as the **pit aperture**. When the secondary wall and the pit border are somewhat thick, the latter one divides the pit cavity into the pit chamber, and the **pit canal**, the passage extending from the lumen of the cell to the pit chamber. In such a case, the pit canal possesses two openings or apertures, one facing the

pit chamber (**outer aperture**), and the other directed towards the cell lumen (**inner aperture**); the former is usually small and circular, while the latter is large and lense-shaped or linear. In a fully developed bordered pit, there is a slight thickening of the central portion of the closing membrane, called the **torus**, and the thin portions may be perforated by numerous minute openings. The closing membrane may be in the median position, or in the lateral one, so as to close the mouth of the pit by the torus. In the latter position, diffusion between two cells becomes minimum. Bordered pits are specially associated with water-conducting channels, but rarely may be found growing in association with living cells.

In some cases, a bordered pit occurs in association with a simple pit instead of another bordered pit, thus forming a **half-bordered pit-pair**. It is found when a living parenchyma with a simple pit is in contact with a dead xylem vessel with a bordered pit in the corresponding area of the common wall, the two pits being separated by a closing membrane, with a weak or no torus. It may retain the median position, or may bulge to one side.

Sometimes, in angiospermous vessels, minute outgrowths or processes project inwardly from the border of a bordered pit into the pit chamber, thus giving the pit a sieve-like appearance. These processes are highly refractive, and are variable as regards their shape, size, and number. In a half-bordered pit, they occur only in the bordered side of the pit. Bordered pits having such processes are termed as **vestured pits** (Bailey, 1933).

Crassulae (Fig. 195) are bar-like or circular thickenings of the primary wall, that partly encircle the bordered pits. They are nothing but margins of primary pit fields covered by secondary wall layers. They are seen in surface view of the pits in properly stained preparations.

Formerly the terms 'bars of Sanio' and 'rims of Sanio' were attributed to the crassulae, but at present, they have been discarded.



FIG. 195. CRASSULAE

CHEMICAL NATURE OF THE CELL WALL

The substance of the cell wall may remain as cellulose throughout its existence, or it may be modified, soon after its formation, in different ways to meet special requirements. The modification is either a case of chemical change, or infiltration, or addition of new different substances, thus changing the nature of the original walls. In all modifications; either all the cell-wall layers or any of these alone may be affected. The various processes involved are as follows :

LIGNIFICATION. Lignification is a process by which the cellulose wall is impregnated with **lignin**. All the three layers of the cell wall, the intercellular layer, the primary wall, as well as the secondary wall, are affected by lignification. The impregnation starts generally in the intercellular layer, and gradually proceeds in a centripetal manner to the primary and secondary wall layers. After lignification, the cell walls are said to be **lignified**. Lignin, which is a chemically complex substance, is hard, elastic and though readily permeable to water, it cannot absorb or retain much of the same in its substance. Cells with lignified walls are usually dead, and such cells are found in the supporting and conducting tissues of plants, such as fibres and wood. The exact importance of lignification is not yet clearly explained. However, it may be said that it increases hardness, strength, durability, and elasticity without the loss of permeability of the walls.

CUTINIZATION AND CUTICULARIZATION. Cutinization is the process by which the old cellulose cell walls are infiltrated with **cutin**, and such walls are said to be **cutinized**. Cutin is a complex fatty substance. It is highly elastic and extensible. Cutinized cell walls are found in the external parts of plants, such as epidermis ; sometimes, the walls of the sub-epidermal cells are also affected. Usually, the outer walls become cutinized, but sometimes, the lateral walls, and rarely, the inner walls are also involved. Cutinized cell walls are not only firm but also less permeable to water and gases, and thus they diminish the loss of water from the surface of the plant.

The aerial parts of the outer surface of the epidermis is covered by a thin layer of cutin forming the **cuticle**, and the

process is known as **cuticularization**, which is quite different from the cutinization process.

Tests : (1) Cutin turns yellow or brown with chlor-zinc-iodine solution. (2) It turns yellow-brown with sulphuric acid and iodine. (3) It turns yellow with caustic potash. (4) It turns pinkish with Sudan III.

CUTICLE. It is a layer of cutin covering the surface of the aerial parts of the plant body. It is thin and feebly developed in young parts, and in plants inhabiting shady and moist places, but is thick and strongly developed in mature plant parts, as well as in plants growing in dry and sunny localities. Its thickness in the leaves and fruits of the same plant may differ according to the seasonal variations.

The cuticle is a secretion of the epidermal and sub-epidermal cells. Droplets of cutin may pass through minute pores on the outer wall, or these may be formed in the deeper-lying cells, and passing along the radial walls finally reach the surface. The surface is always smooth during the early stages ; when mature, it may be roughened by cracks and ridges (**cuticular pegs and ridges**).

The development of the cuticle is mostly followed by the cutinization of the cells below. The radial and inner walls of the epidermal cells as well as the walls of the underlying cells become more or less cutinized.

Some fruits, such as plum, pumpkin, *etc.*, when ripe, possess a thick cuticle, which helps in the conservation of water in them and in the maintenance of their keeping qualities. Thus, fruits with thick cuticle can keep better than those with a thinner one.

SUBERIZATION. It is a process by which **suberin** is intercalated between the particles of the old cell-wall substance, and such walls are said to be **suberized**. Suberin is fatty in nature, Suberized cell walls are usually found in the internal parts of plants, such as cork cells. Suberized cell walls render the cells impermeable to water and gases.

It is to be noted that both cutinization and suberization involve infiltration with wax or wax-like substances, so that the walls are made more or less impervious to water and gases.

MUCILAGENOUS CHANGE. The cellulose cell walls sometimes become **mucilaginous** in nature. Mucilage, when dry, is hard and horny, but when moistened, it absorbs a large quantity

of water, becomes greatly increased in bulk and gelatinous in consistency. Hence, mucilage has a great capacity for retaining water. Mucilage is found in the seed coat of many seeds, e.g., *Plantago ovata* (Fam. Plantaginaceae), *Salvia coccinea*, *Ocimum basilicum* and *Lallemantia royleana* of Fam. Labiatae, etc., of which the first one yields *isaphgul* and the last three are the sources of *topmari*. It is also found in the flowers and fruits of members belonging to Fam. Malvaceae. Mucilage, when present, in the cell wall often serves as a means of storage of water, hence, it occurs in the leaves of desert plants. The mucilage in seeds assists in fixing them to the soil during germination. The mucilage, which is abundant in the submerged water plants, is regarded as the means of protection against animal foes.

- Tests :* (1) Mucilage turns violet with sulphuric acid and iodine.
(2) It turns deep blue with methylene blue.

MINERALIZATION. Soon after the formation of the cell walls, mineralization begins by the process of impregnation by inorganic salts. The chief of these are silica and salts of calcium,

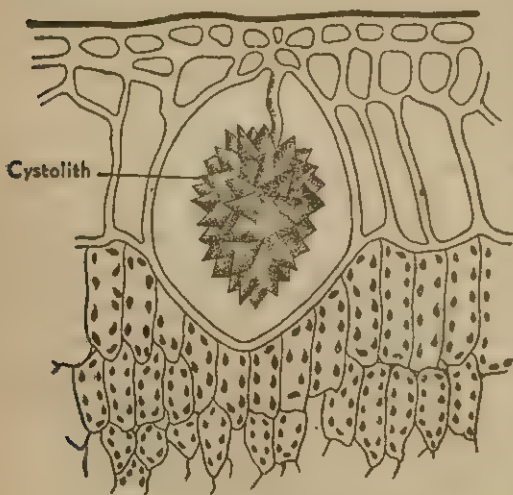


FIG. 196. T. S. OF INDIA RUBBER
LEAF SHOWING CYSTOLITH.

mainly calcium carbonate. Silica is found in the superficial cell walls of the stems of *Equisetum*, grasses, sedges, etc., and gives a considerable firmness to the wall. Silicification and calcification make the wall harder and at the same time brittle.

Some plants develop on the wall of some of the epidermal cells peculiar calcified

localized thickenings, which are known as **cystoliths** (Fig. 196). When fully formed, cystoliths are plainly stalked and found

hanging from the cell wall into the lumen of the cell. Cystoliths are peculiarly developed in a few families, such as Urticaceae, Moraceae, etc., particularly in some species of *Ficus*, e.g., India rubber plant (*Ficus elastica*), banyan (*Ficus benghalensis*), etc. In these cases, some enlarged cells (lithocysts) of the innermost layer of the multiple epidermis of the leaf are provided with curious cellulose projections containing irregular crystals of calcium carbonate, and hanging from the thickened outer wall of the cells project into the cell cavity.

CELL FORMS

The cells assume different forms due to unequal growth: when the growth is uniform, the cell is *spherical* or *round*. When it is greater at the extremities than at the sides, the cell is *oval* or *oblong*. When growth takes place only in one direction, either horizontal or vertical, the cell becomes *elongated*. The different kinds of cells that are found in the permanent regions* of a plant are as follows:

PARENCHYMA. The cells are more or less isodiametric, i.e., equally expanded in all directions. A parenchyma cell is usually *polygonal*, which seems to be the primary and natural form of cells. In some cases, these may be rounded or oval in shape. When these



FIG. 197. SCLERENCHYMA
A, a group of fibres in t.s.;
B, a single fibre in l.s.;
C-D, tracheids.

*For detailed discussions, refer to Chapter III.

cells unite to form tissues, they, as a rule, leave **intercellular spaces** between them. Other forms are *muriform* or brick-shaped, as is found in the epidermis, cork cells, *etc.*, elongated, and *stellate* or star-shaped, as is found in the cells of the midrib of banyan leaf.

COLLENCHYMA. It is a kind of parenchyma consisting of somewhat elongated cells, whose walls are irregularly thickened.

SCLERENCHYMA* (Fig. 197). The cells are generally much longer than broad. Mainly, *two* types of sclerenchyma cells are recognized, viz., *fibres* and *sclereids*. **Fibres** are greatly elongated cells with narrow, pointed opposite ends, with their walls uniformly thickened, and usually provided with simple pits. **Sclereids** have various forms, *e.g.*, rounded, polyhedral, short cylindric, *etc.*, or they may be quite irregular in outline. The cells are dead, and their walls usually become so much thickened and lignified that a very small lumen is left. Sometimes, the walls of the sclereids may be suberized instead of being lignified. They are also characterized by the presence of pits, which are very small, rounded or tubular, and often branched.

All the aforesaid types of cells are found organized into tissues, named according to the peculiar types of cells of which these are composed.

*On account of their dove-tailed arrangement (*i.e.*, in the fashion of the arrangement of feathers in the tail of a dove), the sclerenchymatous fibres are sometimes also designated as the **prosenchyma**.

CHAPTER III

THE TISSUES

Plants, like animals, grow and multiply. When a plant is growing, there is a continuous formation of new cells in the growing parts. When there is reproduction, new cells are also formed. There can be neither growth nor reproduction without the formation of new cells. Cells that keep up the growth of the plant and carry on reproduction do not, however, arise as independent bodies, but are always formed from the mother cells. From these mother cells new cells are produced, and these daughter cells, in their turn, give rise to other new cells, and this process goes on as long as the plant is alive and able to carry on its functions. These cells ultimately constitute a **tissue**. The body of an adult plant is always composed of various kinds of tissues, which are partly mature and partly juvenile in nature. The latter is always located at the growing regions only.

Thus, a *tissue* is usually defined as a *group of similar and united cells performing a common function and having a common origin*. Sometimes, this term is also applied to a more complex group of cells, which differ considerably from one another as regards form and function, but all of them together form a functional unit. Such a tissue is called a **complex tissue**, as distinguished from the former **simple** type. The names of tissues are often derived from the types of cells of which the tissue is made up.

The cells in a tissue are either fitted closely together in such a way, so as to leave no opening or space between them, or the so-called intercellular spaces may develop. According to the mode of origin, the intercellular spaces are of *two* kinds: **schizogenic** and **lysigenic**. When schizogenic, intercellular spaces arise due to the splitting of the adjoining cell walls, and when lysigenic, these are formed due to the complete dissolution of the cells themselves. Most of the intercellular spaces contain air, but under certain conditions, water or various excreted products, such as gums, resins, etherial oils, mucilage, *etc.*, may be found in them. Schizogenic intercellular spaces really form the ventilating system

of the plant, since these contain air, while the lysigenic cavities contain water or various excretory products.

KINDS OF TISSUES

The plant body usually consists of *two* kinds of tissues : vegetative and reproductive. The former are broadly divided into *two* groups, based on the stage of development : (a) **meristematic**, and (b) **permanent**. At the growing regions of the vegetative organs of plants there is but only *one* type of tissue, the cells of which are essentially alike as regards their structure and function. This is known as the **primordial meristem** or **promeristem**, since it contains within itself all the future tissues of a plant body in an undeveloped or primordial condition. By its subsequent growth and differentiation, directly or indirectly, all primary permanent tissues are derived. It is only in fungi that a 'tissue' is derived due to the inter-weaving of filamentous structures, called *hyphae*, and this hyphal tissue is known as **plectenchyma**.

The primordial meristem is soon differentiated into *three* regions of tissues, known as the **protoderm**, the **procambium strands**, and the **fundamental** or **ground meristem**. The three regions together form the **primary apical meristems**, which, on further differentiation, give rise to **primary permanent tissues** (Figs. 198 & 199) in the older or permanent portions of the stem or root.

THE MERISTEMS

THE PRIMORDIAL MERISTEM OR PROMERISTEM

It has already been pointed out that the primordial meristem is found at the growing regions, and from this all other parts of higher plants are derived. The cells are characterized by their small size, comparatively large nuclei, dense cytoplasm, high chromaticity, very thin cellulose walls, absence of insoluble reserve materials, and the power of repeated cell divisions. The cells are generally polyhedral and intercellular spaces are not evident. As the cells divide, some of the daughter cells formed by these divisions begin to enlarge and divide again, and as a result, the growing tip moves forward. At the extreme tip the cells remain

meristematic, but most of the cells behind the tip, sooner or later, become differentiated into *three* well-defined regions, called the *protoderm*, the *procambium* and the *fundamental* or *ground*

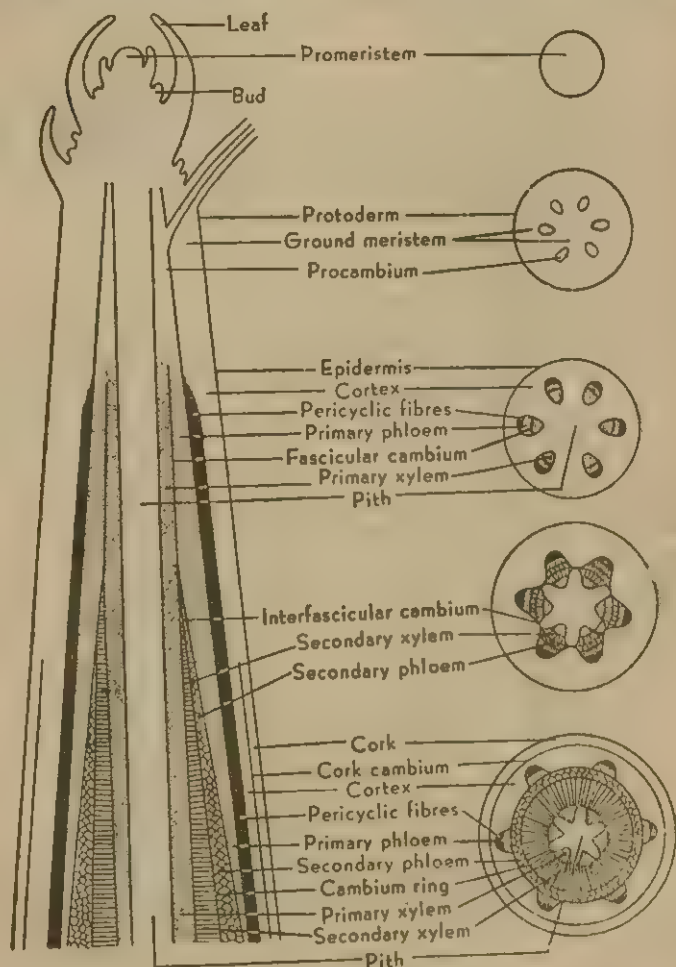


FIG. 198. L. S. OF THE APICAL REGION OF A SHOOT SHOWING GRADUAL DIFFERENTIATION OF TISSUES

(Modified after Hill, Overholts & Popp).

meristem. In the cells of these regions the divisions become less and less frequent, and finally, they cease completely to form pri-

mary permanent tissues. It is to be noted, however, that the products of divisions of the primary meristems do not all give rise to primary permanent tissues. Some of them may remain meristematic throughout their life.

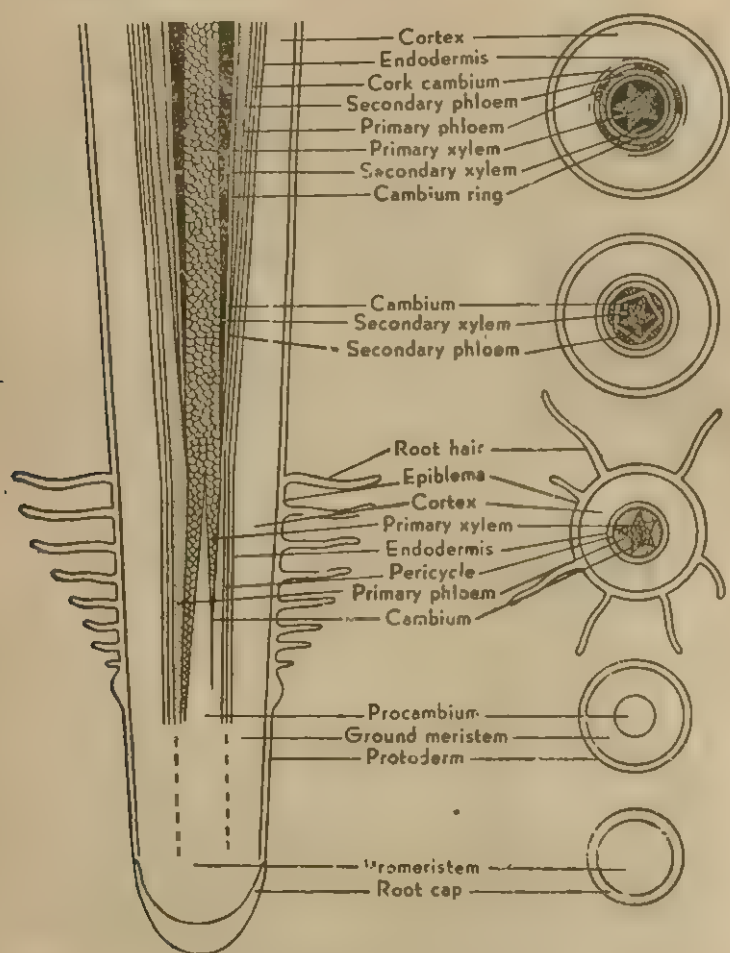


FIG. 199. L. S. OF THE APICAL REGION OF ROOT SHOWING GRADUAL DIFFERENTIATION OF TISSUES

(Modified after Hill, Overholts & Popp).

THE PROTODERM. This constitutes the outermost cellular layer, whose cells divide, usually radially, and after a time, give

rise to the **epidermis**. In some cases, tangential divisions of the cells take place forming a **multiple epidermis**, as in *Ficus*. In roots, the protoderm gives rise to the **epiblema** or **piliferous layer**.

THE PROCAMBIUM. In dicotyledonous stems, it occurs in the form of a ring, which later on splits up into a number of isolated strands arranged in a circle. From each strand a **vascular bundle** develops, consisting of phloem, cambium and xylem. But in monocotyledonous stems, these procambium strands are scattered irregularly, and in roots, there is but one central procambium strand. In some stems, by the gradual increase of procambium strands, a complete cylinder is formed, whose outer layer forms the **pericycle**.

THE GROUND MERISTEM. This meristem is gradually differentiated into the **cortex**, the **medullary rays**, and the **pith**. In stems, where the vascular bundles are quite separated from one another, the **pericycle** is considered to be derived from the ground meristem.

The cells of all these meristematic tissues soon stop dividing, *excepting the cambium*, and form the primary permanent tissues, such as epidermis, cortex, pericycle, xylem, phloem, medullary rays and pith. Though active cell division stops for a time in the cells of the permanent tissues, yet they possess the capability of cell division under certain conditions, become meristematic again, and form the **secondary meristematic tissues**. In fact, all primary permanent tissues are derived from the primary meristems.

CLASSIFICATION OF MERISTEMS

According to the position (Fig. 200), the meristems can be classified into *apical*, *intercalary* and *lateral* ones. **Apical meristems** are present at the growing points of stems and roots, and due to the activity of their cells, these organs increase in length. In pteridophytes, there is a single cell in the apical meristem, called the **apical cell**, whereas, in the higher plants it is made up of a group of cells. **Intercalary meristems** are portions of apical meristems, which become separated from the apex by the development of intervening permanent tissues along with the gradual elongation of the apical meristem. Thus, they lie between masses of permanent tissues, as found in the internodes of *Equisetum*

and many grasses, and also at the bases of leaves. Their main function is to increase the organ in which they occur (in length). **Lateral meristems** are situated along the sides of the stems and the

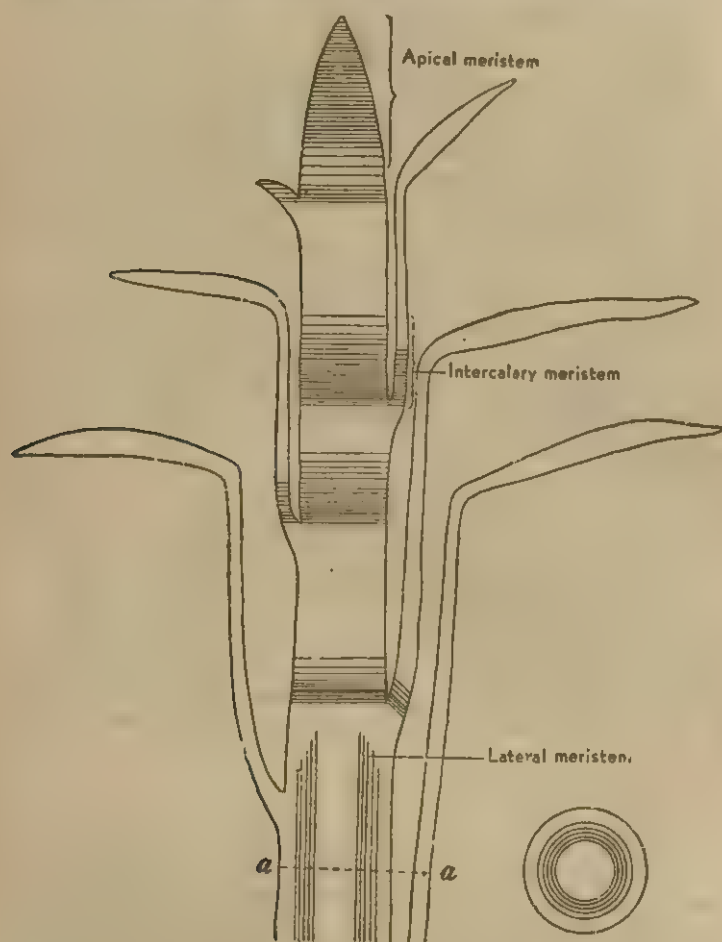


FIG. 200. L. S. OF A GROWING SHOOT SHOWING THE POSITION OF MERISTEMS
(Modified after Eames & MacDaniels).

Right hand figure shows cross section at the level 'aa'.

roots. Their cells divide mainly in one plane, thus causing the organs (in which they occur) to increase in girth; these are characteristics of dicotyledons and gymnosperms. The

fascicular or vascular cambium, and phellogen or cork cambium are examples of such meristems.

According to origin, meristems may be either *primary* or *secondary*. The meristem which persists throughout the life of a plant, and which is present from the time of the embryonic condition of the plant, is called the **primary meristem**. The **secondary meristem**, on the other hand, is derived from the primary permanent tissue under certain conditions. Examples of primary meristems are all apical meristems of stems and roots, vascular (fascicular) cambia of dicotyledons and gymnosperms, and intercalary meristems of monocotyledonous stems. Examples of secondary meristems are interfascicular cambium and cork cambium.

According to the plane of cell division, *three* types of meristems have been recognized : **mass**, **plate**, and **rib meristems**. In the mass meristem, cell division takes place in all planes, and an increase in volume results, as in developing sporangia, endosperm, pith, and cortex of many plants. In the second case, cell division occurs in two planes, and consequently, the increase is in area, as in the developing epidermis and leaf. In the last case, the cell division is in one plane only producing rows of cells, as in the pith and cortex of developing roots and stems.

THEORIES OF ZONATION AND DIFFERENTIATION

The differentiation in meristems brings about a zonation recognized by the number and position of cells, the plane of cell divisions, the size or shape of cells, and the rate of maturation. Several theories dealing with their origin, beginning with that put forward by Wolff (1759), have been proposed from time to time, and a brief account of these is given below.

The Apical cell theory. In many algae, bryophytes, and some pteridophytes, a solitary **apical cell** with a conspicuous vacuole has been found to be present in the growing region. This apical cell is usually pyramidal in shape with occasional variations in form. An apical cell with three cutting faces gives rise to daughter cells (from all its three faces) cut off in a regular alternating sequence. These daughter cells are also vacuolated to some extent. As the presence of a solitary apical cell cannot be demonstrated in the seed plants, this theory has been discarded

in their case. The apical cell theory was later on replaced by the histogen theory.

The Histogen theory. Hanstein (1868, 1870), from his extensive studies on the shoot- and root-apices in phanerogams,

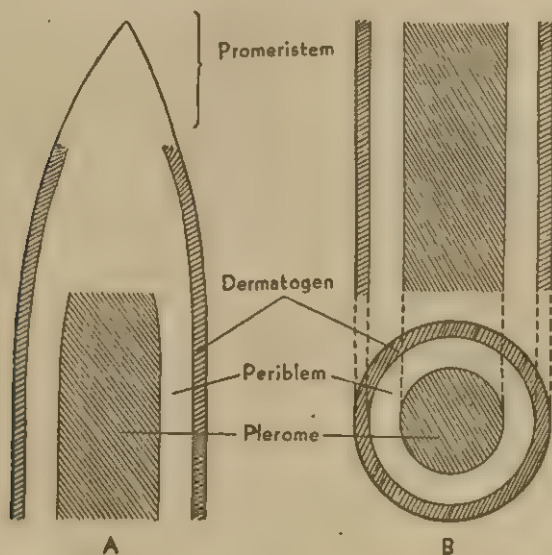


FIG. 201. DIFFERENTIATION OF HISTOGEN LAYERS IN BOTH L. S. AND T. S. (Diagrammatic) (Modified after Eames & MacDaniels).

came to the conclusion that the apex is made up of a mass of meristematic cells having a considerable depth. This mass is differentiable into *three* distinct zones or the **histogens** (Figs. 201 & 202). The outermost layer is known as the **dermatogen**, which gives rise to the epidermis. The second zone, the **periblem**, contributes mainly to the formation of the cortex. The third or the innermost zone, which is termed as the **plerome**, forms the vascular tissues and the pith. But, in some cases, the histogens cannot be differentiated; in some plants, the plerome forms a part of the cortex, or only the pith, or the entire stele. In others, the periblem may form the cortex and a part of the stele, or it may give rise to a part of the cortex only. So, these terms have no great morphological value, but they are still used in connection with the description of the shoot- and root-apices.

The Tunica-corpus theory. The tunica-corpus theory was proposed by Schmidt (1924), and is applied only in the case of the shoot apices in phanerogams. Due to different rates and methods of growth in the shoot apex, two regions of unlike structures are recognized: the **corpus**, the central core, surrounded by an enveloping layer, the **tunica** (Fig. 203). The cells of the corpus are larger than those

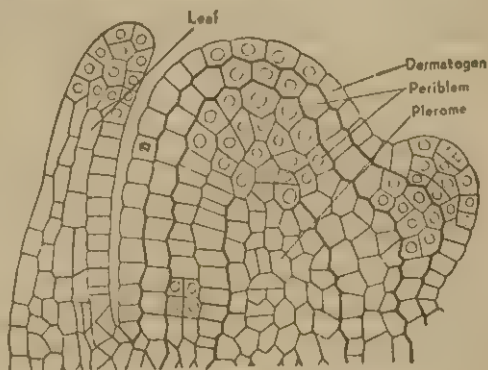


FIG. 202. DIFFERENTIATION OF HISTOGEN LAYERS IN L.S. OF A GROWING SHOOT
(Modified after Eames & MacDaniels).

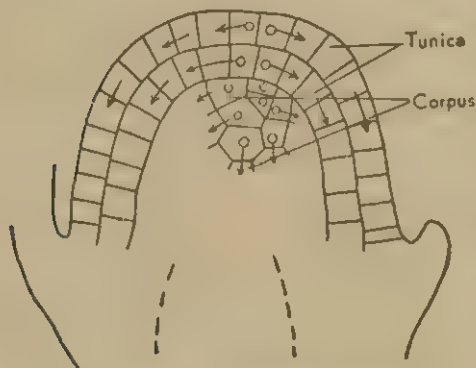


FIG. 203. DIFFERENTIATION OF TUNICA AND CORPUS
(Redrawn from Eames & MacDaniels).

of the tunica; these are irregularly arranged, divide in all possible planes and increase in volume, while the cells of the tunica are small and barrel-shaped, arranged in one or more layers, dividing anticlinally and increasing in surface area. These regions vary in their sizes and limits. The corpus as well as the tunica may be slender or massive.

Below these initials the cells are gradually differentiated forming the tissues of the primary

body. The corpus may give rise to the pith only, or the stele and a part of the cortex, and the outermost layer of the tunica forms the epidermis.

The two terms are purely non-comittal as regards the nature of the tissues produced by them, and hence, should not be recognized as morphologically or functionally constant regions ; they have served well in understanding the complex shoot apices and early development of lateral organs.

THE ROOT APEX (Fig. 204)

The root apex is usually provided with a root cap, which is the terminal portion of the root tip, covering and protecting the growing point. The apical meristem is short, about 1 mm. beneath the cap. The histogens are usually very clearly marked.

Root apices of Dicotyledons and Monocotyledons. Usually, three groups of initials are recognized in the promeristem. In

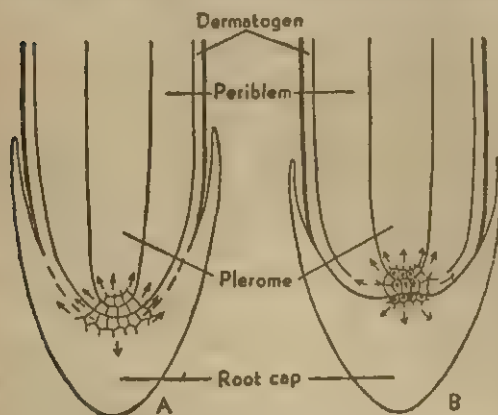


FIG. 204. L. S. OF ROOT APICES
A, of dicotyledon ; B, of monocotyledon
(Redrawn from Eames & MacDaniels).

dicotyledons, the outermost group forms the root cap and the dermatogen, the median group the periblem, and the innermost one the plerome. In monocotyledons, the outermost group of initials forms the cap, the median one gives rise to the dermatogen and the periblem, and the innermost to the

plerome. In some cases, the root cap has an independent origin from a fourth histogen, the *calyptragen*.

The root cap consists of a parenchymatous tissue of short-lived cells, arranged irregularly or in radiating rows. The outer cells, dying and loosened from one another, are destroyed due to the friction of soil particles, and are subsequently replaced by new cells formed from the abutting initials. The loose outer cells are more or less mucilagenous. The cap is present in all roots, except in some parasites and aquatic plants.

PRIMARY PERMANENT TISSUES

The primary permanent tissues, which are derived from the apical meristems, consist of cells which have assumed a more or less definite form and size, and have ceased to divide, but they possess the capability of dividing under certain conditions. The cells may be living or dead, thin-walled or thick-walled, and the cell wall either remains as cellulose or variously modified during differentiation. They usually contain intercellular spaces in between the cells and may be grouped as *simple*, *complex* and *special tissues*.

SIMPLE TISSUES

The simple tissues consist of a group of similar type of cells forming an uniform mass and performing the same functions. The common simple tissues in plant bodies are **parenchyma**, **collenchyma**, and **sclerenchyma**, and these names are derived from the cell types of which these are composed.

PARENCHYMA. (Fig. 205). Parenchyma is the most common type of primary permanent tissue, which consists of parenchyma cells having diameters essentially equal. The cells are usually characterized

by their round, oval or polyhedral form, abundant active protoplasm, the capability of cell division (even when the cells are permanent), and with intercellular spaces in between them. The cell wall is thin and made up of cellulose. Paren-

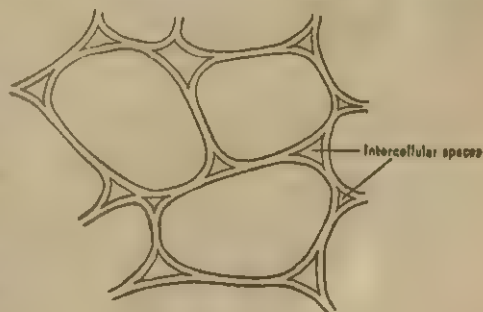


FIG. 205. PARENCHYMA

chyma has been called the **ground** or **fundamental tissue**, since all specialized tissues develop from it. This tissue makes up the greater part of the plant body, *viz.*, cortex, pith, medullary rays, mesophyll of leaves, pulp of fruits, *etc.* Its functions are mainly food manufacture, food storage, and slow conduction of food; hence, it forms, primarily, a nutritive tissue.

When parenchyma contains chloroplasts, it is called **chlorenchyma**. In the epidermis of stems, roots, leaves, and other organs, the walls of the parenchyma cells become cutinized. In some cases, these may also be suberized. Their functions are mainly affording protection and prevention from evaporation or diffusion of watery fluids.

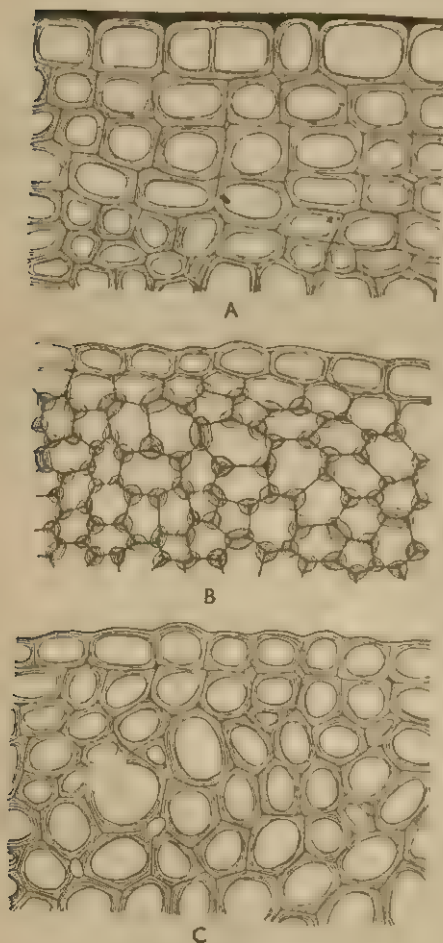


FIG. 206. DIFFERENT TYPES OF COLLENCHYMA

A, lamellar ; B, angular ; C, lacunar.

COLLENCHYMA (Fig. 206). Collenchyma consists of somewhat elongated cells, whose primary walls are thick but not lignified. The cells contain protoplasm, thus indicating a close relationship with parenchyma cells. In regions where both collenchyma and parenchyma occur side by side, very frequently intergrading forms are noted.

Collenchyma is, as a rule, found in the peripheral regions of stems and leaves. Occasionally, it may also occur in the cortex of roots, which are particularly exposed to light. It acts as the first supporting tissue in some plant organs, such as, stems, leaves, and parts of flowers, while in some herbaceous plants, it is the only supporting tissue present. Collenchyma usually occurs in the sub-epidermal position, either as a continuous band or in the form of discrete patches. In stems and petioles having

protruded ribs, collenchyma becomes well developed in the ribs.

Collenchyma cells may be either short and prismatic, or elongated resembling the fibres (attaining a length of up to 2 mm.) with tapering ends. In transverse sections, both these types appear to be polygonal. The thickenings on the walls of collenchyma cells take place unevenly. In the most common form the thickenings occur at the corners or angles, where a number of cells join together. This is known as the **angular type** of collenchyma, and is found in *Cucurbita* and other members of Fam. Cucurbitaceae, *Polygonum* and *Rumex* of Fam. Polygonaceae, *Beta* of Fam. Chenopodiaceae, *Ficus* and *Morus* of Fam. Moraceae, *Boehmeria* of Fam. Urticaceae, *Cannabis* of Fam. Cannabinaceae, *Begonia* of Fam. Begoniaceae, and others. On the other hand, in plants like *Clerodendrum* (= *Clerodendron*) of Fam. Verbenaceae, *Sambucus* of Fam. Caprifoliaceae, *Eupatorium* of Fam. Compositae, *Rheum* of Fam. Polygonaceae, etc., the thickenings chiefly occur in the tangential walls, the radial walls remaining thin. As a result, the thickenings appear as elongated bars, and this type of collenchyma is known as the **lamellar type**. A third type, called the **lacunar type** of collenchyma, is found in *Malva* and *Althaea* of Fam. Malvaceae, *Heliotropium* of Fam. Boraginaceae, *Salvia* of Fam. Labiatae, *Lactuca* of Fam. Compositae, etc. In this case, there are prominent intercellular spaces present, and the thickenings lie around these spaces.

SCLERENCHYMA. The cells of sclerenchyma are characterized by the extreme thickening and hardening of the walls due to lignification, simple pits, more or less uniformly thickened walls as to leave a very



FIG. 207. SCLERENCHYMA
A, group of fibres ; A', t.s. of the same ; B, a fibre-tracheid ; B', t.s. of the same.

small lumen, mostly without protoplasm but not always so, and with a very low percentage of water content. It is a common practice to classify sclerenchyma into *two* chief categories, viz., *fibres*, and *sclereids*.

Fibres (Fig. 207, A) are groups of greatly elongated cells usually with narrow, pointed opposite ends, or their walls are uniformly thickened and generally with unbordered pits which are small, rounded or slit-like. The cells, when mature, are usually dead, and with a narrow lumen due to the extreme thickening of the wall. The cell walls are usually hard and lignified, but sometimes may be wholly or partly of cellulose, or may even be mucilaginous. Fibres are mainly of *two* types : **xylem fibres**, and **extraxylary fibres**. The fibres of the cortex, pericycle and phloem are common examples of the latter type, and they have simple pits, whereas, the fibres in the xylem are called *xylem fibres*, which have reduced bordered pits. The function of the fibres is purely mechanical, *i.e.*, they give strength, rigidity, and protection to the plant. The sclerenchyma tissue may be developed anywhere in the stem. Thus, they may be found as the bundle sheath in monocotyledonous stems, as the bundle cap in the stem of sunflower, as the whole of the pericycle in *Cucurbita* stem, as the hypodermis in pine leaf, as isolated patches in the cortex of palm stem, as wood fibres in xylem, and as bast fibres in phloem.

Between typical fibres and normal tracheids all intergrading forms, called **fibre-tracheids** (Fig. 207, B), occur. In fibre-tracheids, pits are smaller than those of tracheids. In the phylogenetic development of the fibre, the wall-thickening is increased with a corresponding reduction in the diameter of the lumen, the number and size of pits, and the length of the cell.

Sclereids (Fig. 208). Sclereids are specialized lignified cells, which are generally found in the cortex and pith of dicotyledonous and gymnospermous plants. They are also associated with the fibres of phloem and xylem. Sclereids may be few or abundant in the leaves of some tropical plants. They also occur very frequently in various seeds and fruits, thus giving strength and rigidity to the seed coats, as well as to the nut shells and endocarps of stony fruits.

Sclereids are extremely variable as regards forms and structures. Tschirch (1899), Haberlandt (1914), and Foster (1949),

however, arbitrarily classify them into *four* broad groups as follows :

Brachysclereids or Stone cells. These cells are parenchyma-like, short, more or less isodiametric, and found in the cortex, phloem, and pith of stems like tobacco (*Nicotiana tabacum*) of Fam. Solanaceae, as well as in the pulp of fleshy fruits like guava (*Psidium guayava*) of Fam. Myrtaceae, pear (*Pyrus communis*), of Fam. Rosaceae, etc.

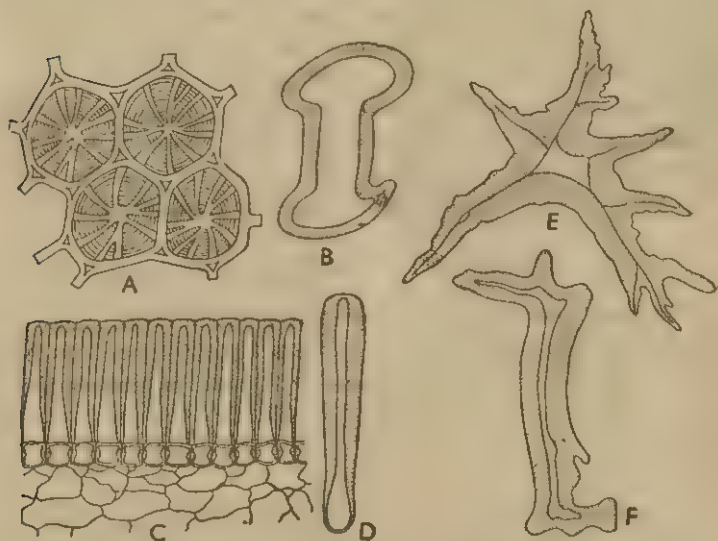


FIG. 208. DIFFERENT TYPES OF SCLEREIDS

A, brachysclereids from the flesh of pear ; B, macrosclereid from the seed coat of pea ; C, macrosclereids from the outer part of the seed coat of *Phaseolus* ; D, one from C magnified ; E, astrosclereid from the leaf of *Trochodendron* ; F, osteosclereid from the leaf of *Mouriria*,

Macrosclereids. The cells are elongated, rod-shaped, and forming a palisade-like layer in the epidermis of the seeds of leguminous plants like pea (*Pisum sativum*), and mung (*Phaseolus mungo*).

Osteosclereids. The cells are columnar and bone-shaped with bulging ends, and are usually found in association with macrosclereids. These can be found in the leaves of *Mouriria* (Fam. Melastomaceae).

Astrosclereids. The cells are branched in various ways forming star-shaped bodies, and are found in some dicotyledonous leaves like tea (*Thea chinensis*) of Fam. Theaceae, *Trochodendron* (Fam. Magnoliaceae), etc.

Sclereids are dead cells, and sometimes contain tannin and mucilage. The walls become greatly thickened and lignified, but occasionally may be suberized or cutinized. They are also characterized by the presence of pits, which are very small, rounded or tabular, and often branched. The lumen is very small.

In some plants, the leaves and petioles are commonly subjected to a shearing strain, which is met with by the arrangement of single cells having very thick and lignified cell walls. Such solitary cells, having purely mechanical functions, are known as **idioblasts**, which commonly occur in the leaves of tea and petioles of blue water lily. These cells also differ in form, contents and peculiar wall thickenings from the neighbouring cells.

COMPLEX TISSUES

Complex tissues consist of a complex group of more than one types of cells working together as a unit. The vascular tissues, xylem and phloem, are the only complex tissues of great importance, which have been considered below.

XYLEM

The cells of this tissue, after undergoing extreme modifications during the growth processes, become differentiated in the primary stage into four kinds of elements, viz., *tracheids*, *vessels* or *tracheae*, *xylem (wood) parenchyma*, *xylem (wood) fibres*, and *fibre-tracheids*.

Tracheids (Fig. 197, C-D). Tracheids are elongated dead cells, with comparatively blunt ends, having their lumen large and empty, and mostly angular in cross section. The walls are in most cases lignified, bordered-pitted and large in gymnosperms but small in angiosperms, and with annular, spiral, reticulate and scalariform thickenings in pteridophytes. These cells are disposed in the organ parallel to its long axis. They are associated with the water-conducting tissues in the vascular bundles of gymnosperms and pteridophytes. In angiosperms, however, their function is chiefly mechanical due to the presence of vessels

or tracheae. But in plants like *Amborella trichopoda* of Fam. Monimiaceae (Bailey & Swamy, 1948), and *Sarcandra* of Fam. Chloranthaceae (Swamy & Bailey, 1950), where vessels are completely absent, the tracheids help in water conduction in addition to their normal mechanical function. Tracheids represent the fundamental cell type in xylem, and probably make up the entire xylem of the primitive plants, as well as of the pteridophytes (excepting *Selaginella* and *Pteridium*), and gymnosperms (Fig. 209) (excepting Gnetales) of the present day.

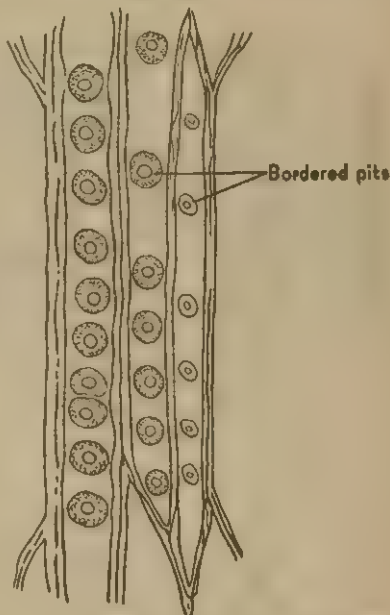


FIG. 209. TRACHEIDS FROM THE WOOD OF *Pinus*.

Vessels or tracheae. The vessels are long, tubular structures, formed by the total absorption of the end walls from a chain of procambium cells, or these may be derived from fused tracheids. There is a rapid enlargement of these cells at their meristematic stage (Fig. 210). At maturity, there is a slow disintegration of the protoplast, perforation or total dissolution of the end walls, and subsequent lignification and deposition of thickenings on its lateral walls. The various types of thickenings found include annular, spiral, scalariform, reticulate, and pitted. The vessels are so very highly specialized that they are mainly concerned in water conduction and mechanical support to the plant. The thin places in the walls also serve for ready passage of liquids from one vessel to another, while the thickenings not only stiffen the wall, but also enable the vessels to withstand external pressure and prevent their collapsing. Vessels are characteristics of angiosperms, but with a few exceptions, as in some plants belonging to the families Chloranthaceae, Magnoli-

aceae, Cactaceae, as well as in some aquatic and parasitic plants. Among gymnosperms, they are only present in the group Gnetales.

The limits of vessels vary with the nature of the plants, types of xylem, and the rate of growth of the organs. In climbing

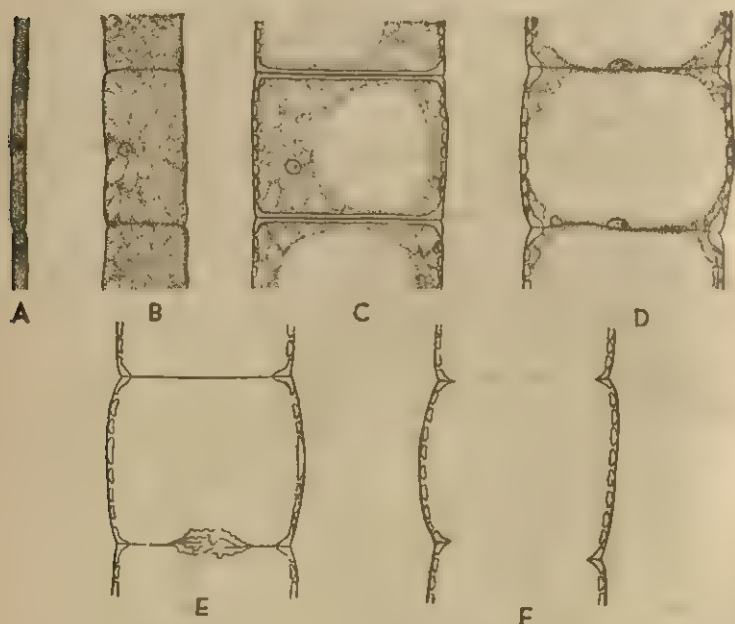


FIG. 210. STAGES IN THE DEVELOPMENT OF VESSEL.
(Redrawn from Holman & Robbins).

plants and some trees, they may be several metres long, but usually they are only a few centimetres in length. The widest vessel may be about 1 mm. in diameter, as in maize and many lianes. It is, however, interesting to note that in many magnoliaceous plants, the length and breadth of the mature vessels remain practically the same as those of the procambium cells.

The main difference between a tracheid and a trachea is that the former is an imperforate cell communicating with one another by bordered pit-pairs on the lateral walls, while the latter is provided with distinct perforations (Fig. 211) on the end walls, so that, a series of these elements form an open tube-like structure.

The perforations may be **simple** (*i.e.*, with a single large hole), or **scalariform** (*i.e.*, with a series of small parallel holes).

Xylem (wood) parenchyma. Xylem parenchyma is made up of more or less elongated parenchyma cells, placed end to end. The walls are either thin or thick, more or less strongly lignified, and may be simple- or bordered-pitted. When the xylem parenchyma lies in association with tracheids or tracheae, its walls are always provided with bordered pits. On the other hand, in a group of xylem parenchyma cells, only simple pits occur on their walls. They are present in the primary as well as secondary woods, and in the secondary medullary rays of dicotyledons and gymnosperms. In some gymnosperms, as in *Pinus*, *Araucaria*, etc., they are absent. They are associated with food storage, conduction of water, directly or indirectly, and giving mechanical support to the plant.

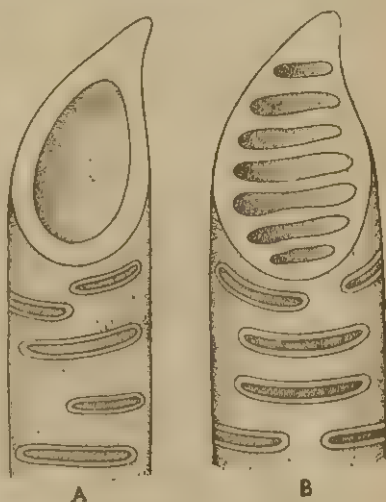


FIG. 211. PERFORATIONS
A, simple ; B, scalariform.

Xylem (wood) fibres. The structure and functions of xylem fibres have already been discussed before.

Fibre-tracheids. The fibre-tracheids are the transitional forms in between fibres and tracheids. They are generally like tracheids with blunt ends, and are provided with simple or bordered pits. They resemble the fibres in having thickly lignified lateral walls and narrow lumina. Their function is purely mechanical.

PHLOEM

The elements of which the phloem is made up (phloem elements) differ in different kinds of plants. In higher plants,

it usually consists of *sieve tubes*, *companion cells*, *phloem parenchyma* and *phloem (bast) fibres*. In some cases, stone cells and various types of secretory cells are also present. In other cases, all these types of elements do not occur together. In gymnosperms and pteridophytes, it consists of sieve tubes and phloem parenchyma only, and in monocotyledons, it consists of sieve tubes and companion cells.

Sieve tubes (Figs. 212 & 213). A sieve tube develops from a longitudinal row of vertically elongated, thin-walled, living cells,

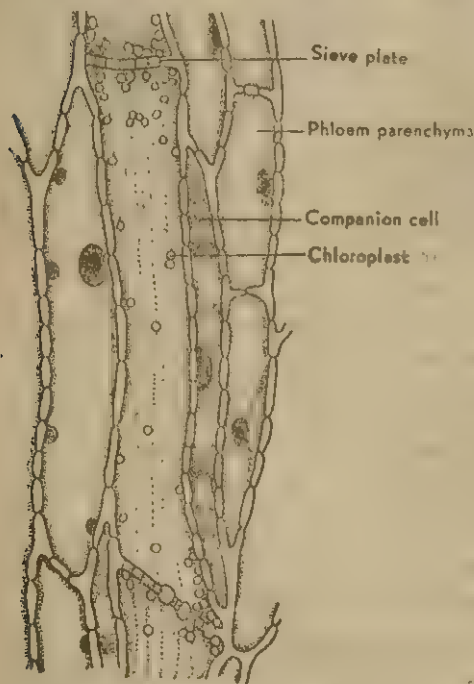


FIG. 212. STRUCTURE OF PHLOEM IN L.S.
(Redrawn from Holman & Robbins).

which are separated from one another by more or less thickened end walls. These walls become perforated by many openings to form the **sieve plates**. In gymnosperms and pteridophytes, sieve plates also occur along the side-walls of the sieve tubes, and, in some cases, the sieve plates are obliquely placed. In each fully developed sieve tube, there is a conspicuous central vacuole and a peripheral layer of cytoplasm containing a few leucoplasts and scattered starch grains,

but without any nucleus. Prominent cytoplasmic connections are found to traverse through the openings of the sieve plates. The cell sap contains protein substances in solution giving it a slimy nature. The chief function of sieve tubes is conduction of elaborated foods, such as carbohydrates and proteins, from

the leaves down the stem to the roots and other parts of the plant body, where these are either used up directly or stored for future use of the plant.

The function of the sieve tubes ceases either temporarily or permanently by the formation of a colourless substance, called **callose**, whose chemical nature and mode of deposition are not yet properly known. The presence of callose can only be detected with the help of some special staining reagents, like aniline blue, resorcin blue, etc. The callose usually forms a cap-like mass, known as the **callus** or **callus pad**, on the surface of the sieve plates. Most of the callus permanently stops the activity of the sieve tubes, but, when temporary or seasonal, it may be dissolved, and the sieve tube again renews its activity.

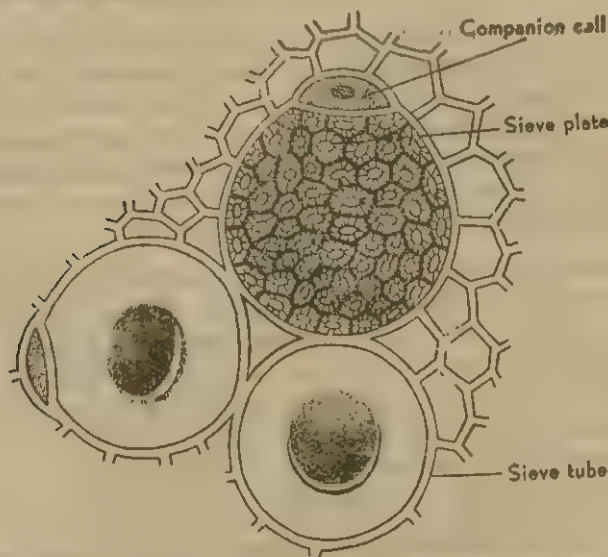


FIG. 213: STRUCTURE OF PHLOEM IN T.S.
(Redrawn from Holman & Robbins).

Companion cells. Adjacent to the sieve tubes there are elongated, somewhat asymmetrical, and specialized parenchyma cells, which remain connected to the sieve tubes. On the contrary, they contain some proteinaceous matter. These are known as the **companion cells** (Fig. 212). Each companion cell contains richly granular cytoplasm, some vacuoles, and a cons-

picuous nucleus, but without any starch grain. These companion cells are present in almost all the angiosperms, excepting some primitive, woody dicotyledonous plants (Bailey & Swamy, 1949). They are lacking in gymnosperms and pteridophytes. Probably they assist sieve tubes in the conduction of food.

A vertical row of procambium cells divides longitudinally producing a double vertical row of cells with numerous primary pit fields in the walls. The cells of one row enlarge, their walls thicken, pit fields turn to sieve areas, callose develops around the cytoplasmic connecting strands, the nucleus disintegrates, the vacuoles enlarge and coalesce, and a vertical row of these cells form a more or less continuous tube connected by sieve plates. The cells in the other vertical row form the companion cells.

Phloem parenchyma. The cells of phloem parenchyma, at the time of differentiation from the procambium, consist of vertically elongated cells, which, later on, increase in their cross diameter. Their chief functions are : translocation of sugars and readily diffusible proteins, storage of protein substances, and helping in transporting food substances from the sieve tubes to the medullary rays and xylem parenchyma.

Phloem (bast) fibres. Phloem fibres are of frequent occurrence in the secondary phloem of angiosperms. These are, however, absent in pteridophytes, some gymnosperms, and a few herbaceous angiosperms. The structure and functions of phloem fibres have already been discussed. The phloem fibres of some plants like jute (*Corchorus capsularis* and *C. olerius*) of Fam. Tiliaceae, rami (*Boehmeria nivea*) of Fam. Urticaceae, etc., are of great economic importance.

Apart from the functions of conduction and storage of food as well as mechanical support, the phloem, as a whole, is important in connection with upward translocation of mineral nutrients in solution. But, how this takes place is not yet clearly understood.

SPECIAL TISSUES

This group includes various secretory tissues, such as secretory cells, glands and laticiferous ducts, which are characterized by their conspicuous contents and special functions. These tissues

are responsible for the secretion of various substances, such as gums, resins, etherial oils, nectar, and other substances of a similar nature. Frequently, isolated secretory cells are also found in almost any tissue, such as cortex, pith, xylem, phloem, *etc.* The secretory tissues are discussed under the following heads :

Secretory cells (Fig. 214). The secretory cells are of *two* kinds : (a) there are some secretory cells, such as stinging hairs, e.g., *Fleurya* and *Urtica* of Fam. Urticaceae, *Tragea* of Fam. Euphorbiaceae, nectaries, epithelium of resin- and oil-canals, *etc.*, where the secretions are irregularly exuded ; (b) in other cases, the secretion is stored within them. The former is often called the **excretory cell**, which is characterized by the presence of richly granular protoplast and a prominent nucleus.

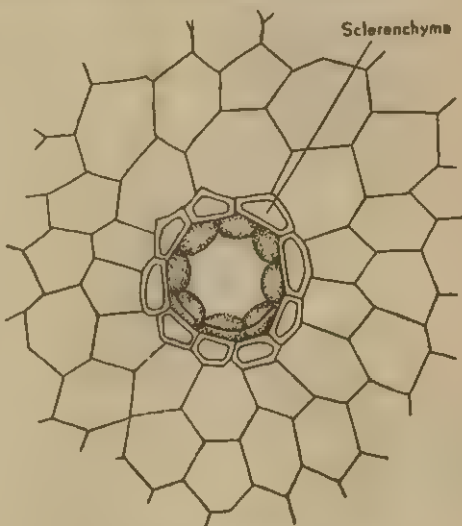


FIG. 214. SECRETORY CELL

The latter type, the **secretory cell**, has inconspicuous cytoplasm and a large cell-cavity filled with the secretion products, as found in ginger, many ferns, *etc.*

Glands (Fig. 215). The secretory cells are often grouped together to form a special structure, called a **gland**. Based on location and form, *three* types of glands may be recognized as follows : (a) **superficial type**, found on the outer surface of the plant body (e.g., *Begonia* of Fam. Begoniaceae, *Passiflora* of Fam. Passifloraceae, *Anthocephalus* of Fam. Rubiaceae, *etc.*) or arising from it forming hairs (**trichomes**) and scales (e.g., *Cucurbita* of Fam. Cucurbitaceae, *Grewia* of Fam. Tiliaceae, *Kleinhovia* of Fam. Sterculiaceae, *Platanus* of Fam. Platanaceae, *Nicotiana* of Fam. Solanaceae, *Gossypium* of Fam. Malvaceae, *Olea* of Fam.

Oleaceae, etc.) ; (b) **internal globular type**, consisting of cells forming a globular structure (as are found in the members of the Fam. Rubiaceae, particularly on the adaxial surface of the leaf base and on the interpetiolar stipule) ; and (c) **internal tubular type**, formed either schizogenously (e.g., resin ducts of pine), or

lysigenously (e.g., pericarp of *Citrus*). When schizogenous in origin, the secretory cells form a sheath or covering, known as the **epithelium**, around an intercellular canal, called the **duct**, which becomes filled with secretions of these cells, as in the resin ducts of pine.

Glands are mostly digestive in function, since they secrete digestive enzymes, and hence, are also known as **digestive glands**. Nectar-secreting glands are known as **nectaries**. There are also some other types of glands.

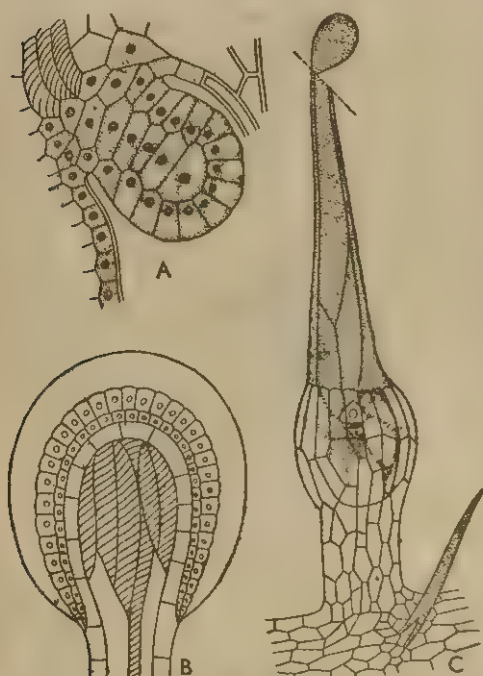


FIG. 215. GLANDS

A, of *Drosera* ; B, of *Nepenthes* ; C, of *Urtica*.

Digestive glands. The digestive glands secrete enzymes for digestion (*intra-cellular digestion*), and these are characteristics of the majority of living plants. But, in insectivorous plants, there are special glands ; these secrete protein-digesting enzymes, which act on various small, entrapped insect-bodies. The products of digestion are finally absorbed by the plants (*extra-cellular digestion*). Examples are *Drosera* (Fam. Droseraceae), *Nepenthes* (Fam. Nepenthaceae), and other insectivorous plants.

Nectaries. These specialized glands occur in different regions of floral parts, as well as on other structures, such as bracts, and

consist of specialized cells for the secretion of nectar. These nectaries are characteristics of entomogamous plants.

Hydathodes (Fig. 216). The hydathodes are organs for secreting water, often along with various salts in solution, in the liquid form. They are present on the leaves, commonly in the margins or apices of plants, which grow under conditions of low temperature, abundant water-content of the soil, and humid atmosphere. They become active, when the hydrostatic pressure in the water-conducting tissue reaches a certain

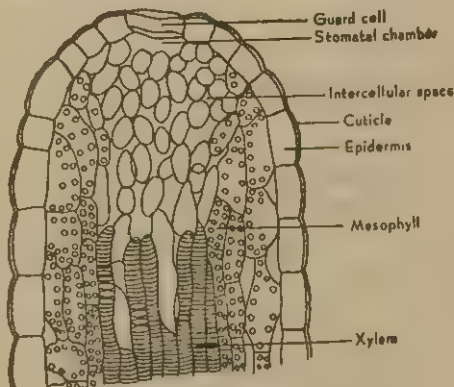


FIG. 216. HYDATHODE
(Modified after Haberlandt).

limit due to suppressed transpiration, and protect the intercellular air-spaces from being flooded.

Very often in the morning, after a warm and damp night, drops of water may be seen on the margins or apices of leaves of many plants, such as aroids, grasses, *Tropaeolum*, etc., and are usually mistaken for dew drops. Each of these drops marks the position of a hydathode.

A hydathode may be a unicellular or a multicellular epidermal outgrowth, directly connected with the water-conducting tissue (xylem). More commonly, it consists of a mass of thin-walled mesophyll cells with abundant intercellular spaces, called the **epithem**, which lies between the epidermis and the bundle end. The epithem remains filled with water, and opens into one or more sub-epidermal chambers, communicating with the exterior through one or more water stomata. The cells are small and devoid of chloroplasts.

Resin ducts (Fig. 217). The resin ducts are tube-like passages for the secretion and conduction of resin. They are abundantly

present in the gymnosperms particularly, and also in several families of angiosperms.

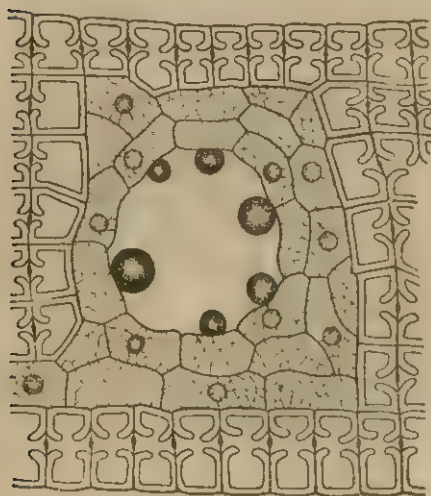


FIG. 217. RESIN DUCT OF *Pinus*

Laticiferous ducts.

Laticiferous ducts are of two kinds : (a) *latex vessels* or articulated latex ducts, and (b) *latex cells* or non-articulated latex ducts. They are characterized by the presence of latex.

Latex vessels (Fig. 218). The latex vessels are formed due to the cell wall fusions of elongated living cells, which take place early in the primary meristematic condition, the separating walls being



FIG. 218. LATEX VESSELS OF *Argemone*.

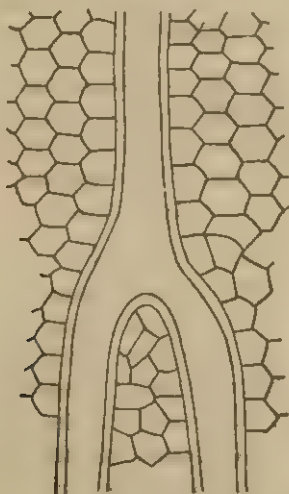


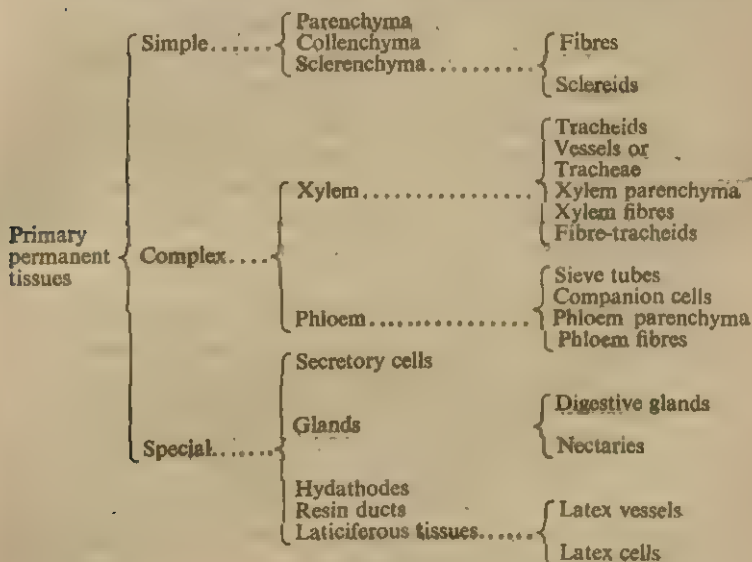
FIG. 219. LATEX CELL OF *Pedilanthus*.

more or less completely dissolved. They are living, and

generally possess lateral branches, which, when meet, fuse with one another by the absorption of their end walls. Latex vessels are characteristics of the families Papaveraceae, Cactaceae, Musaceae, Araceae, *etc.*, and of the genus *Hevea* of Fam. Euphorbiaceae.

Latex cells (Fig. 219). The latex cells are structurally cells containing numerous nuclei. Each tubular cell develops from a single meristematic cell, which gradually elongates and branches, keeping pace with the growth of the plant. In the embryos of certain plants, these cells sometimes occur, and when they grow, the cells elongate and ramify profusely throughout the plant body. The branches do not anastomose, as in the case of latex vessels. The latex cells are found in the families Urticaceae, Asclepiadaceae, Apocynaceae, Moraceae, and in the majority of genera belonging to Fam. Euphorbiaceae.

The primary permanent tissues may be tabulated as follows :



CHAPTER IV

THE TISSUE SYSTEMS

Basing on the structural continuity or functional similarity or both together, the tissue units are generally grouped into **tissue systems**. The structural complexity of a plant is, thus, dependent on the tissue systems present therein. Botanists could not come to an agreement as regards the classification of cells, tissues, and tissue systems. The old classification of the tissue systems, as proposed by Sachs (1875), is, however, followed in general. He grouped the various tissues under *three* categories : (i) the **epidermal** or **tegumentary tissue system**, (ii) the **vascular** or **fascicular tissue system**, and (iii) the **fundamental** or **ground tissue system**. Haberlandt (1914)* suggested that the tissues should be grouped under *twelve* different systems, based on their anatomico-physiological functions, like absorption, conduction, support, *etc.* Lundgardh (1922) proposed another system of classification, also based on anatomico-physiological concept, in which these *two* major groups of tissue systems, *viz.*, the **coherent tissue systems**, and the **dispersed tissue systems**, are considered. The former are made up of continuous cell collections, while the latter are composed of individual cells or groups of cells, forming 'islands' within the various coherent systems.

I. The Epidermal tissue system. The epidermal tissue system consists of the outermost protective layer or **epidermis**, often including its various outgrowths and openings, which are present in different parts of the plant body, such as roots, stems, leaves, flowers, fruits, *etc.* It is derived from the primary apical meristem, known as the protoderm.

II. The Vascular tissue system. The vascular tissue system chiefly consists of complex tissues, such as xylem and phloem, constituting the **vascular bundles**, which are mainly con-

* A brief account of a few of Haberlandt's tissue systems has been given in Chapter VIII.

cerned in the conduction of sap containing various raw food materials, as well as of elaborated foods. This system also gives mechanical strength and support to the plant. The vascular tissue system is derived from the procambium strands, and its arrangement varies in different organs of the same plant, as well as in different groups of plants.

III. The Fundamental tissue system. The fundamental tissue system forms the main bulk of the plant body and lies below the epidermis of the different organs of plants. It is chiefly made up of parenchyma cells, and is mainly concerned in the metabolism, storage of food, and partly in the mechanical support of the plant. Sometimes, collenchyma, sclerenchyma, and other tissues may be present. In roots and stems, this system consists of the cortex limited internally by the endodermis or starch sheath, the pericycle, the primary medullary rays, and the medulla or pith. In leaves, this tissue is known as the **mesophyll tissue**, often differentiated into **palisade** and **spongy parenchymas**. These individual tissues have been described in details in the following pages. This tissue system is derived from the fundamental or ground meristem.

The relations between primary apical meristems, primary permanent tissues, and the tissue systems are tabulated below :

| | <i>Primary apical meristems</i> | <i>Primary permanent tissues</i> | <i>Tissue systems</i> |
|---|--------------------------------------|--|---------------------------|
| | Protoderm..... | Epidermis..... | Epidermal |
| Promeristem or Primordial meristem | Fundamental or Ground meristem | { Cortex (limited internally by endodermis) Pericycle Medullary rays Pith or Medulla | Fundamental |
| | Procambium strands..... | Vascular bundles..... | Vascular |

THE PRIMARY BODY

A vascular plant starts its life with the zygote. On germination, the zygote gives rise to an embryo, which is made up of meristematic cells only. Gradually, as the embryo develops into an adult plant, different types of cells, tissues, and tissue systems make their appearance in its various organs, like root, stem, leaf, flower, fruit, and seed. The different plant parts, arising from the apical meristems, usually grow in length. The total growth of an organ from the start up to its complete expansion from the apical meristem is regarded as its **primary growth**. The plant body, which is thus formed due to primary growth, is known as the **primary plant body**. Subsequently, secondary tissues are added to the primary body by the **secondary growth**, resulting in the formation of the **secondary body**. The primary body reveals the following structures.

THE EPIDERMIS

The epidermis consists of the outermost layer of the primary plant body, and is made up of parenchyma cells. Each cell, when young, contains cytoplasm and a nucleus, but is usually without chloroplasts. In ferns and some aquatic plants, particularly in monocotyledonous ones, however, chloroplasts occur frequently. The cell sap is generally colourless, but in some fruits, it is coloured. This layer is more or less continuous, except at the regions of stomatal openings. It is derived by the differentiation of the protoderm cells, whose outer walls undergo modifications due to infiltration of waxy substances, known as **cutin**, hence, rendering them impervious to water and gases. In some cases, a distinct cuticle may be present. The epidermis usually consists of a single layer of cells (**simple epidermis**), but sometimes, as in the leaves of India rubber, banyan, oleander, *Begonia*, *Peperomia*, etc., and in the areial root of orchids, it becomes many-layered, *i.e.*, **multiple**, due to the tangential division of the protoderm cells. Sometimes, parts of the epidermis become structurally modified to form the stomata, secretory tissues (as nectaries), root hairs, *etc.*, to perform special functions. The epidermis of the root is called the **piliferous layer** or **epiblema**, since it bears root hairs.

In the epidermis of the majority of monocotyledonous leaves (excepting Potamogetonaceae, Alismataceae, Hydrocharitaceae, etc.), and particularly in the members of the family Gramineae, there are some large, highly vacuolated, mainly water-containing cells with cutinized outer walls, covering large areas, or occurring as small patches in the grooves. These cells are known as **bulliform** or **motor cells** (Fig. 220). They may appear in a fan-like pattern in the cross section of the leaf. Their function may be to bring about the unfolding of the developing leaf due to sudden expansion, or to bring about the hygroscopic movement of mature leaves by changes of turgor, or simply storage of water.

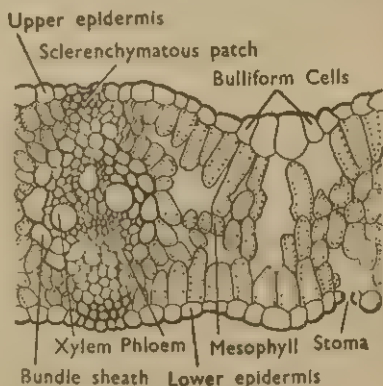


FIG. 220. T. S. OF WHEAT LEAF SHOWING BULLIFORM CELLS.

EPIDERMAL OUTGROWTHS

The chief appendages of the epidermis are known as **trichomes** (Fig. 221). Sometimes, the term **emergences** is employed to designate the trichomes. But, as de Bary (1884) points out, the two terms should not be used synonymously, because the emergences are developed both from the epidermis as well as from the hypodermis. The trichomes, on the other hand, are produced only by the epidermal cells. This distinction is, however, not always sharply marked out, as very frequently intergrading forms are met with. The trichomes are either unicellular or multicellular, and simple or branched outgrowths of various forms, which are usually classified into the following *four* common types.

Hairs. Structurally, the hairs are either unicellular or multicellular. The root hairs are simple and unicellular epidermal outgrowths. The stinging hairs of *Urtica* (nettle) and other glandular hairs are complex multicellular structures. The cells of the hairs may be living or dead. The cell wall is usually made

up of cellulose and is thin, but sometimes it may be thickened, lignified or cutinized.

Hairs perform various functions. Root hairs absorb water containing mineral salts in solution from the soil. Hairs on leaves and stems are chiefly meant for reducing transpiration and the intensity of illumination. Hairs on the stigmas catch hold of

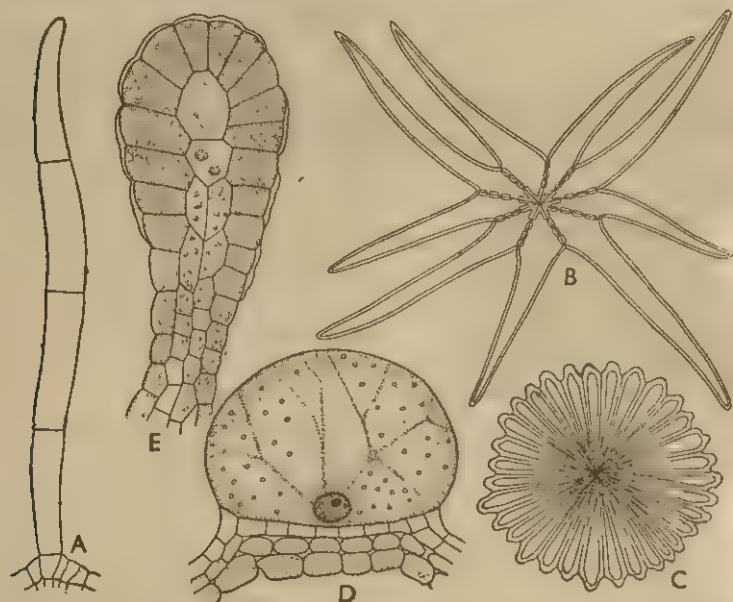


FIG. 221. DIFFERENT FORMS OF TRICHOMES

A, ordinary hair of tobacco ; B, stellate hair of *Sida* ; C, peltate hair of *Olea* ; D, water vesicle of *Mesembryanthemum* ; E, glandular trichome on stipule of *Viola*.

pollen grains and help in pollination, while those on seeds and fruits help in their dispersal. The glandular hairs protect the plants by storing secretory or excretory products, but those, which are found in the insectivorous plants, give out enzymes by means of which the insect-bodies are digested. The stinging hairs protect the plants against the attack of herbivorous animals, and sometimes, hairs assist climbing plants to catch hold of their supports.

Scales or peltate hairs. These are specialized trichomes, which possess discoid body, usually provided with a short stalk, as in *Olea* of Fam. Oleaceae (Fig. 221, C).

Colleters or glandular trichomes. The multicellular and stalked, specialized trichomes with a globular head, found in the leaves, bud-scales and stipules of many genera belonging to the families Rubiaceae, Apocynaceae, Asclepiadaceae, etc., are termed as 'colleters' by Hanstein. The outer cells of the globular or knob-like head are secretory in nature.

Bladders or water vesicles. In some plants, like *Mesembryanthemum crystallinum* of Fam. Aizoaceae (Fig. 221, D), the trichomes are highly expanded, water-containing cells. These cells occur frequently on the young leaves and stems, and look like so many translucent drops of ice. Hence, the plant is popularly known as the 'ice plant'.

EPIDERMAL OPENINGS

There are two types of epidermal openings: *stomata* and *water stomata*.

Stomata (Figs. 222-225). The epidermis of the aerial parts

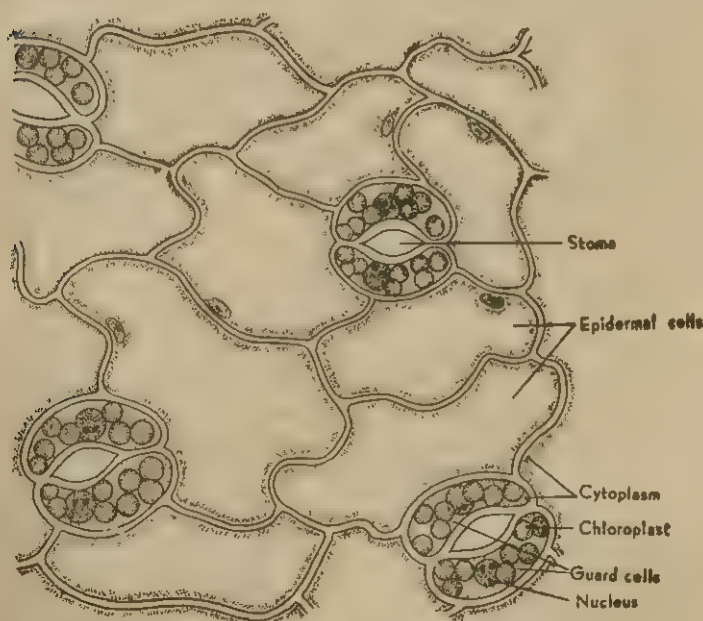


FIG. 222. STOMATA IN SURFACE VIEW
(Redrawn from Holman & Robbins).

of plants is not continuous. There are many minute pores

in it, and each pore is bounded by two specialized, semilunar epidermal cells, known as the **guard cells**. The whole structure, consisting of the pore together with the guard cells, is called a **stoma**, which is concerned with transpiration, as well as the gaseous interchange between the atmosphere and the internal tissues of plants. The opening of the stoma leads into a big air cavity, the **respiratory cavity** or **sub-stomatal air chamber**, surrounded by the sub-epidermal cells. The respiratory cavity is in communication with the intercellular spaces. The guard cells contain cytoplasm, nucleus and green plastids.

Considerable differences are found in the construction of the guard cells and the mechanism of opening and closure of the stomata.

In the *Amaryllis* type, common in the dicotyledons and monocotyledons, the cell walls of the guard cells surrounding each

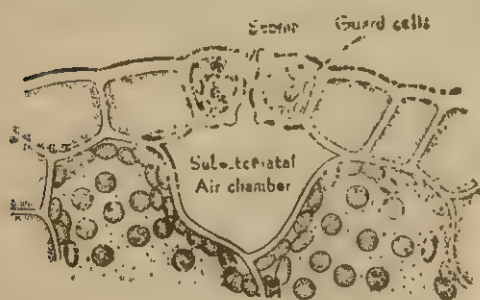


FIG. 223. A STOMA IN SECTIONAL VIEW (T.S.).

opening are, in most cases, of greater average thickness than elsewhere. Usually, the wall of each guard cell furthest away from the opening is more extensible, and bulges out when the cell becomes turgid, consequently, dragging the inner wall

surrounding each opening along with it. When the cells become flaccid due to the loss of turgidity, the cell walls relax, so that, they fall upon each other, and thus, the opening is diminished in size or closed altogether.

In the *Grass* type, common in the families Gramineae and Cyperaceae, the guard cells are dumb-bell-shaped, whose wider ends are thin-walled, and the middle regions are narrow with strongly thickened outer and inner walls (Fig. 224). When the cells become turgid, their oval, thin-walled ends expand, and bring about a separation of the rigid middle portions, thereby opening the stoma.

In the *Mnium* type, commonly found in the mosses and ferns, the walls of the guard cells are more or less uniformly thickened, or the wall furthest away from the pore is more thickened, and the guard cells are oval in cross section. When the turgor increases, these cells tend to become round (in cross section), thus separating the closing walls of the pore.

Intermediate types also occur, and several modifications are found in the xerophytes.

There are *two* theories, which attempt to explain the condition of guard cells during their movements, a brief account of which is given in the following few lines :

(a) **Carbohydrate transformation theory.**

During the day time, due to photosynthesis, sugar accumulates in the guard cells, and makes the cell sap more concentrated than that in the adjacent epidermal cells. The guard cells absorb water from the neighbouring mesophyll cells by osmosis, become turgid, and cause an opening of the stoma due to unequal expansions on their two faces.

Since the cell sap is alkaline in nature, the starch is converted into sugar. At night the sugar in the cell sap is converted into starch, making the cell sap less concentrated, whereby the guard cells become flaccid, and by losing water close the stoma. In the absence of photosynthesis, the cell sap becomes slightly acid, due to the accumulation of carbon dioxide, and the sugar is transformed into starch.

(b) **Colloidal hydration and dehydration theory.** During the day time, the alkalinity of the cell sap brings about a swelling of the colloidal cell contents of the guard cells, whereby they (guard cells) bulge out, and open the stoma. On the other hand, at night, the acidity of the cell sap brings about a shrinkage of the colloids, and thus, the stoma is closed.

The guard cells can, thus, increase or decrease the size of the opening, and can regulate the various gaseous interchanges between the atmosphere and the internal tissues. The functions



FIG. 224. STOMATA OF GRASSES

A, surface view ;
B, in sectional view (T.S.).

of respiration, transpiration and photosynthesis depend largely upon this diffusion of gases.

The modes of arrangement of the surrounding subsidiary cells in relation to the guard cells have led to a classification of the stomata in dicotyledons into the following *four* types (Metcalf & Chalk, 1950).

I. Ranunculaceous or anomocytic (irregular-celled) type (Fig. 225, A). In this type, the stoma is surrounded by a

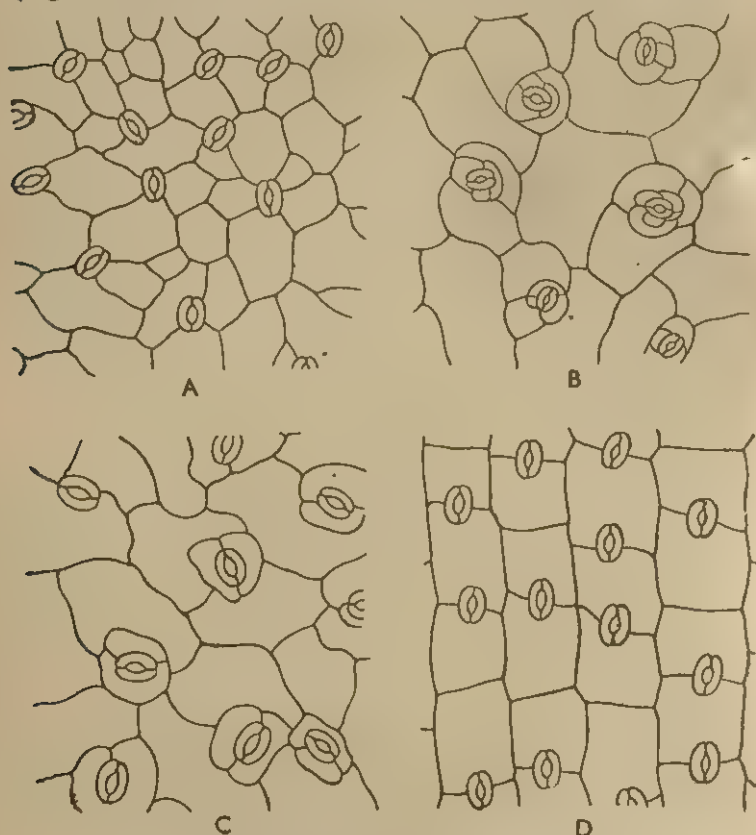


FIG. 225. DIFFERENT TYPES OF STOMATA

A, ranunculaceous or anomocytic type ; B, cruciferous or anisocytic type ;
C, rubiaceous or paracytic type ; D, caryophyllaceous or diacytic type.

limited number of subsidiary cells, which are irregular in size, shape or form from the remaining epidermal cells.

II. Cruciferous or anisocytic (unequalled-celled) type (Fig. 225, B). Each stoma is surrounded by three subsidiary cells, of which one is smaller in size than the other two.

III. Rubiaceous or paracytic (parallel-celled) type (Fig. 225, C). In this case, the stoma is associated on either sides with one or more subsidiary cells lying parallel to the long axis of the guard cells or the stomatal pore.

IV. Caryophyllaceous or diacytic (cross-celled) type (Fig. 225, D). The stoma in this type is surrounded by a pair of subsidiary cells. The common wall of the latter is at right angles to the guard cells.

Previously, it was believed that a particular type of stoma is a characteristic feature of a definite species. But, recent studies have nullified the idea. For instance, Sen (1955) has shown in the *Centrospermae*, that even in the same leaf of a particular species, different types of stomata with their intergrading forms occur frequently.

Stomata may be developed on all green parts of plants, being more abundant in leaves, where they may occur as many as 100-300 per sq. mm. Sometimes, they become very numerous, as in *Brassica* (600-700 to 2,000 per sq. mm.). Stomata are most abundant on the ventral surfaces of dorsiventral leaves; in isobilateral leaves, they are equally distributed on both the surfaces. In floating leaves, they occur on the dorsal surfaces only, and in submerged leaves and roots, they are not developed at all.

During the formation of a stoma, a young epidermal cell divides into two unequal cells, of which the smaller one is the **guard mother cell**. This mother cell divides by a vertical wall into two guard cells, between which the intercellular passage (the pore) is formed by a splitting of the common wall. The **subsidiary cells** are developed either from the original epidermal cell, or from several adjoining epidermal cells.

Plants are often in danger of losing too much of water by transpiration, which takes place through the stomata. Dry wind, heat, and deficient absorption are the chief sources of danger. When excessive transpiration is threatened, the guard cells become flaccid, and thus, the stomatal openings are reduced or closed

altogether. But those plants, which live in places where constant dry wind and heat prevail, have their stomata protected as follows : they may be covered by hairs ; they may develop a thick cuticle ; they may be sunken in pits or crypts (**sunken stomata**), and the surface on which they are present may be rolled up.

Water stomata. The water stomata are larger than the ordinary stomata, and are chiefly found in aquatic plants. Their guardcells do not contain any protoplasm. Hence, the openings cannot be regulated, and thus, the pores always remain open. The water stomata give out water in the liquid state.

The normal functions of the epidermis are mechanical as well as physiological. Primarily, it protects the inner tissues from mechanical injuries, excessive heat and cold, as well as from the attacks of fungi and bacteria. It helps in transpiration and gaseous exchange, and also acts as the storehouse of water and various metabolic products. The epidermis performs certain subsidiary functions as well. For instance, in plants with cuticularized or waxy epidermal layers, it helps to check excessive loss of water. Where the epidermis is multiple, it behaves as a reservoir of water. Other accessory functions of the epidermis are secretion, absorption, photosynthesis, and possibly, the perception of stimuli. In case of roots, however, the main function of the epiblema is the absorption of water with the help of root hairs.

THE CORTEX

This group of tissues, surrounding the stele, is bounded externally by the epidermis and internally by the endodermis or starch sheath. Its thickness is very variable, and usually, it is made up of parenchyma cells. Intermingled with it may also be present collenchyma, fibres, sclereids, and various kinds of secreting and storage cells. When a few outer layers of the cortical cells lying internal to the epidermis become transformed into a sheet of strengthening tissues, chiefly having a protective function, it is known as the **hypodermis**, and the remaining portion of the

cortex is termed the **general cortex**. In the lower vascular plants, the cortex is generally differentiated into *two* regions, an **outer cortex** and an **inner cortex**. Sometimes, the cortex forms a definite photosynthetic tissue. In roots, in the majority of cases, the cortex is made up of parenchyma only, with conspicuous intercellular spaces. Its chief functions are to give mechanical strength to the plant, to store food and water, and to carry on photosynthesis to some extent.

THE ENDODERMIS

Surrounding the stele on the outside and lying internal to the cortex, there is a single layer of barrel-shaped cells (in cross section), without intercellular spaces, known as the **endodermis** (Fig. 226). Hence, it acts as the *limiting layer* in between the cortex and the stele.

In some pteridophytes, like *Marsilea*, an inner endodermal layer occurs internal to the xylem tissue, thus separating it from the pith. The cells are vertically elongated having transverse end walls. They are living and frequently contain starch grains, but sometimes may contain mucilage, tannin, crystals, etc. Owing to the presence of starch grains, the innermost layer of the cortex of some young angiospermous stems is known as the **starch sheath**. Guttenberg (1943) considers the starch sheath as homologous

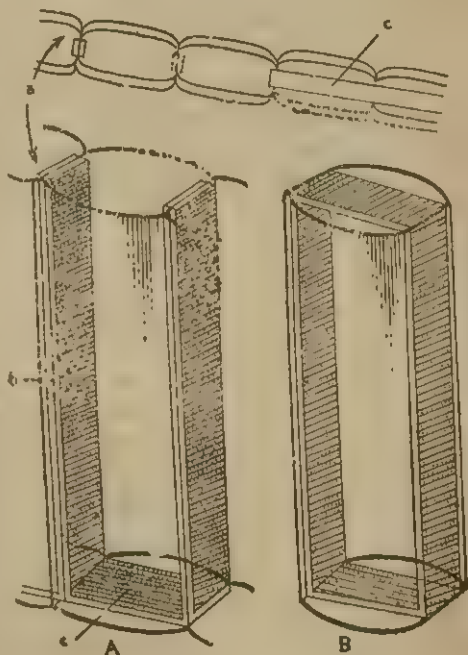


FIG. 226. ENDODERMIS WITH CASPARIAN STRIPS.

with the endodermis, when in stems the former occurs in the position of the latter. The inner transverse as well as the radial walls of the cells of the endodermis have peculiar thickenings (lignified or suberized). The thickening layer occurs in the form of a band, which runs completely round the inner surface of the radial and inner tangential walls of each cell. This thickening layer is known as the **Casparian strip** or **band** (Fig. 226). Thus, when sectioned, these strips appear as dots on the radial walls. In case of roots of monocotyledonous plants, either the entire or the radial as well as the inner tangential walls of the endodermal cells generally become very much thickened with characteristic small, simple pits. Between these thickened cells there occur some thin-walled cells, the **passage cells**, which lie opposite to the protoxylem groups of the vascular bundles, as in the aerial roots of orchids. Through these passage cells the sap absorbed by the root hairs enter the xylem vessels. The endodermis occurs throughout the plant body, particularly in the roots of the vascular plants, and in the majority of pteridophytes. It is very characteristic in the leaves of gymnosperms, but is usually absent in their stems. In angiosperms, it is present mostly in the herbaceous stems, but is absent in the woody stems and leaves in general.

The function of the endodermis has been variously interpreted by different authors. These interpretations are mainly based upon its relation to water and to the vascular elements. It appears to be a water-tight diffusion layer (separating regions of different osmotic pressures), which checks the loss of nutrient solution from the vascular tissue to the surrounding ones. This idea is supported by the facts that the intercellular spaces are always absent, and that the walls are somewhat thickened with lignin, or suberin. The other views are that (i) it is an accessory epidermal layer, purely protective in function, (ii) it is concerned with maintaining the root pressure, (iii) it is the starch sheath, and hence, acts as a storage tissue (in stems), and (iv) it is a sort of air dam, which checks the air-clogging of the water-conducting tissues.

THE PERICYCLE

Lying internal to the endodermis and enclosing the vascular bundles, there is a strip of tissue, known as the **pericycle**. It is

made up of one to several layers of cells. In roots and stems of some aquatic plants, it is completely absent. The pericycle is normally made up of parenchyma cells, but may also be either wholly or partially sclerenchymatous. In roots, it is generally made up of a single layer of parenchyma cells; this layer is very important, because of the fact that it gives rise to a secondary meristematic tissue, the **pericambium**, at the time of secondary growth. The pericycle chiefly performs a mechanical function, but when parenchymatous, it acts as a storehouse of reserve foods.

THE PRIMARY MEDULLARY RAYS

The portions of the ground tissue, lying between the vascular bundles and arising from the ground meristem by vertical and transverse divisions of their cells, are known as **primary medullary rays**. In cross sections, they are found to be made up of slightly elongated parenchyma cells, which either act as storehouses of water and reserve foods, or carry substances in a watery solution inward and outward according to requirements. At the commencement of secondary growth in stems, the interfascicular cambium differentiates from this tissue.

THE PITH OR MEDULLA

Enclosed by the vascular bundles and the primary medullary rays, there lies a mass of living parenchyma cells, which constitute the **pith or medulla**. The cells are rather loosely arranged with conspicuous intercellular spaces, and mostly rounded or cylindrical, with thin cellulose walls. Sometimes, lignified parenchyma cells, and sclereids may be associated with it. In herbaceous plants, the pith may be torn apart, forming a 'hollow pith', as in *Cucurbita*. The chief function of the pith is the storage of starch and fatty substances. Sometimes, it may also store up mineral crystals, mucilage, and various other excretory products.

THE PRIMARY VASCULAR BUNDLES

The narrow, elongated, living cells of the procambium strands, differentiated from the primary apical meristems, by subsequent growth and further differentiations, give rise to such complex

tissues as **xylem** and **phloem**, usually grouped together forming **vascular bundles**. A strip of primary meristematic tissue, known

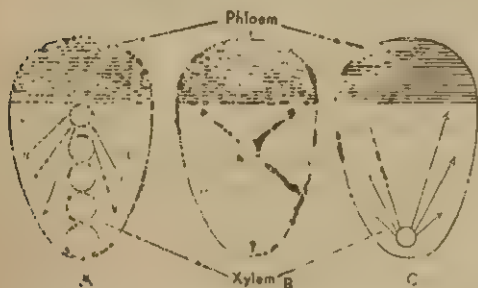


FIG. 227. CENTRIPETAL AND CENTRIFUGAL DEVELOPMENTS OF XYLEM AND PHLOEM.

A, exarch ; B, mesarch ; C, endarch
(Redrawn from Holman & Robbins).

as the **cambium**, is present in between the xylem and the phloem of the stems of dicotyledons and gymnosperms. According to the presence or absence of the cambium, a vascular bundle may be either **open** or **closed** respectively. In case of roots, the xylem

and the phloem do not occur together, but form separate vascular bundles. With reference to the centre of the axis, the xylem groups are either produced centripetally or centrifugally, or both centripetal and centrifugal developments take place (Fig. 227). Accordingly, the xylem groups are known as **exarch** (e.g., in all roots), **endarch** (e.g., in stems of seed plants), and **mesarch** (e.g., in stems and leaves of ferns and cycads) respectively. The phloem group always develops centripetally.

The various tissues and tissue elements of the xylem and the phloem with their respective functions have already been described in detail (*vide* pp. 340-346). The first differentiated xylem and phloem elements are known as **protoxylem** and **proto-phloem** respectively. The protoxylem elements are slender, narrow, and have characteristic wall-thickenings (annular and spiral). The elements of the xylem and the phloem, which are differentiated later, are distinguished as **metaxylem** and **metaphloem** respectively. The walls of the metaxylem elements have characteristic reticulate and pitted thickenings. The primary xylem and phloem consist of both proto- and meta-xylem and phloem elements respectively. The protophloem, in several cases, consists of phloem parenchyma only, but the metaphloem consists of sieve tubes, companion cells, phloem parenchyma, and phloem fibres. In monocotyledons, the primary phloem persists throughout the life of the plant, since the secondary phloem is not formed, and is

of great functional importance. In some dicotyledons, such as *Cucurbita*, the primary phloem persists throughout its life. The primary xylem consists of tracheids, tracheae with annular, spiral, reticulate and pitted thickenings, and xylem parenchyma cells. Xylem fibres are absent in the primary bundles.

With reference to the relative position of the xylem and the phloem in a bundle, the following types (Fig. 228) are recognized.

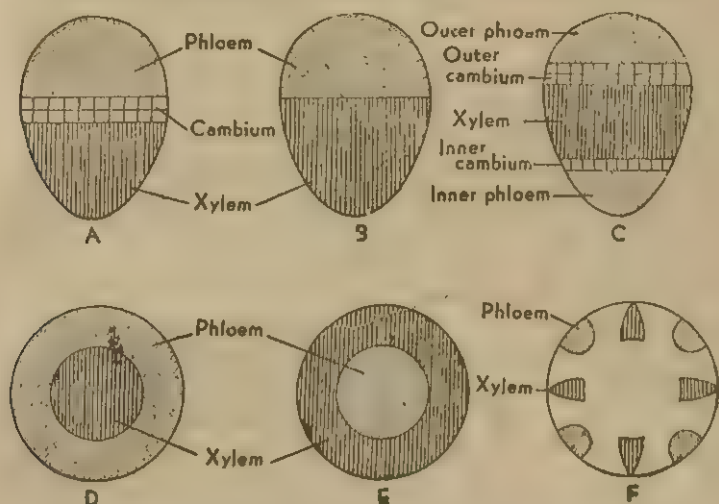


FIG. 228. TYPES OF VASCULAR BUNDLES (Diagrammatic)

A, conjoint, collateral and open ; B, conjoint, collateral and closed ; C, bicollateral ; D, hacrocentric ; E, leptocentric ; F, radial.

Conjoint and collateral. This is the most general type in the stems of monocotyledons, dicotyledons, and gymnosperms. The xylem and the phloem are arranged side by side on the same radius, xylem internal and phloem external. This type of bundle is either **open**, as in dicotyledonous and gymnospermous stems, or **closed**, as in monocotyledonous stems.

Conjoint and bicollateral. When phloem is situated on both sides of xylem, being separated from the latter by strips of cambium in such a way that all these lie on the same radial line, as in the Fam. Cucurbitaceae, Solanaceae, etc.

Concentric. When both xylem and phloem occur together in such a way that the one encloses the other. It may be **hacro-**

centric or amphicribal, i.e., xylem at the centre surrounded by the phloem, as in ferns, or **leptocentric or amphivasal**, i.e., phloem at the centre, surrounded by xylem, as in *Dracaena*, *Yucca*, etc.

Radial. When xylem and phloem from separate bundles and occur on alternate radii in a ring, as in all roots.

LONGITUDINAL COURSE OF VASCULAR BUNDLES (Fig. 229).

The vascular bundles are continuous from the root tips to the extremity of leaves. This course can be followed by the microscopic examination of macerated materials.

The radial bundles of the root are traced to the base of the shoot, where they undergo fusion and twisting through 180° , and then continue upwards as the collateral bundles of the stem. Some of the bundles of the stem may be followed up to the apex (without passing into the leaf) and they are called the **cauline bundles**.

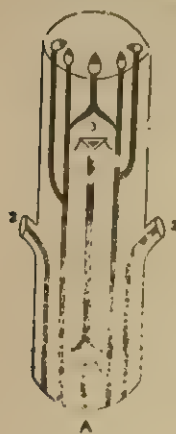


FIG. 229. LONGITUDINAL COURSE OF VASCULAR BUNDLES

A, in dicotyledon ; B, in monocotyledon ; the figures or numbers indicate the positions of leaves.

The main joining bundles, however, pass outwards into the leaves forming the **common bundles**, which are common to both stem and leaf. That portion of the bundle, which connects the bundle of the stem with that of the leaf, i.e., the part of the bundle between the point of its departure from the stele to the base of the leaf, is called a **leaf trace** or **foliar bundle**. One or more leaf traces may enter into the stem from a single leaf.

Usually, each descending bundle of the stem, after twisting or splitting, ends by joining another bundle, which has entered from a lower leaf. The general course differs in different plants, according to the length of the free course of the individual bundles ; the course they follow, the splitting and joining they

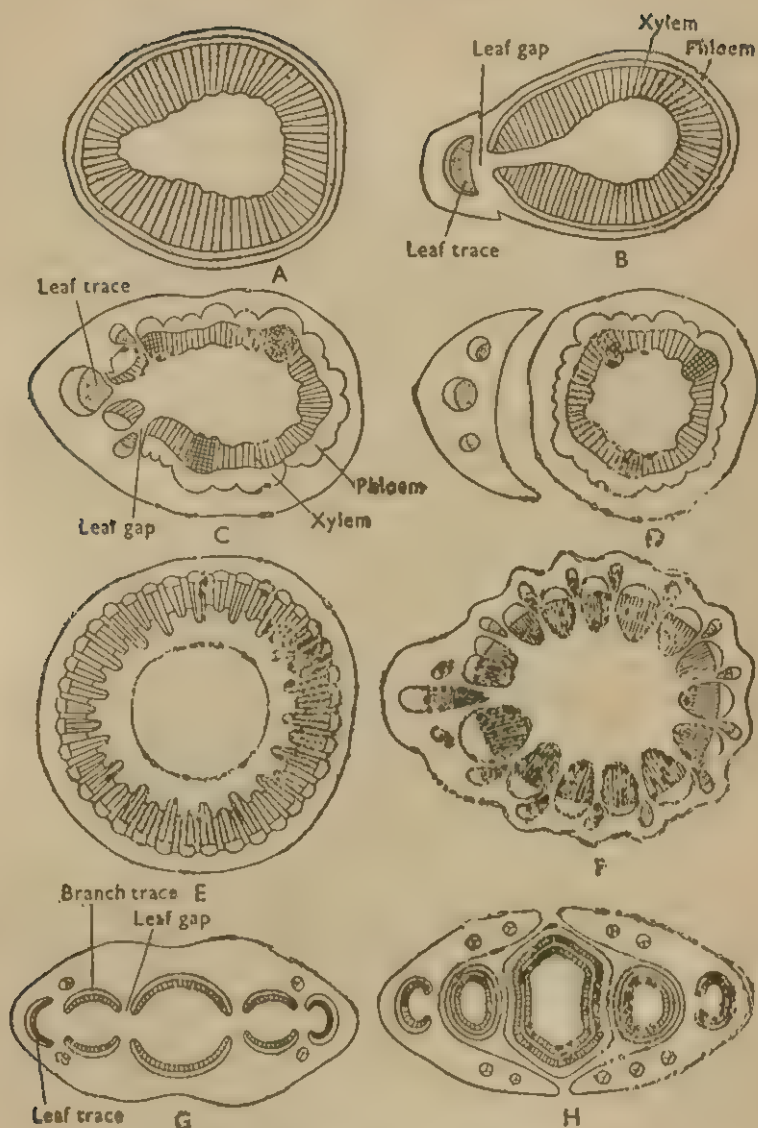


FIG. 230. DIFFERENT TYPES OF NODAL STRUCTURE IN T.S. OF DICOTYLEDONOUS STEMS (Diagrammatic).

A, D, E, t.s. of stems of *Spiraea*, *Salix* and *Rumex*; B, C, F, the same of these plants respectively at the nodes showing unilacunar, trilacunar and multilacunar nodes; G, unilacunar node in t.s. of stem of *Veronica*; H, showing the primary vascular system of a plant body having opposite decussate leaves.

undergo, and their place of entry into the stem are determined by the arrangement of the leaves on the shoot.

In gymnosperms and dicotyledons, all the leaf traces penetrate equally deeply into the stem, and travel down forming rings in transverse sections.

In monocotyledons, the leaf traces penetrate into different depths in the stem, and appear scattered in transverse sections. The bundles first penetrate nearly up to the centre of the stem, then they curve outwards, remain independent and distinct through a number of internodes to fuse ultimately with the other peripheral bundles.

Leaf gaps or lacunae. The leaf gaps or lacunae are formed as a result of departure of the leaf traces from the axial vascular cylinder into the leaves. They are not breaks or empty spaces in the continuity of the axial cylinder, but parenchyma cells interpolated in these regions. Lateral connections exist in the vascular cylinder above and below these gaps.

There are *three* common types of nodes occurring in the dicotyledons on the basis of the number of these lacunae (Fig. 230). In the first or **unilacunar type**, a single leaf trace comes out of the vascular cylinder resulting in the formation of a single leaf gap. In the second or **trilacunar type**, there are three leaf traces from the axial cylinder leaving three gaps at the node. The last or **multilacunar type** is characterized by more than three to many gaps caused by a corresponding number of leaf traces.

Branch traces and branch gaps. Branches of the vascular plants, as a rule, develop in the axils of leaves, and their vascular supplies are intimately connected with the vascular cylinder of the axis. In dicotyledons and gymnosperms, the vascular traces entering into the branch are known as the **branch traces**. The gap, which is caused in the axial cylinder due to the departure of the branch trace, is called the **branch gap**.

CHAPTER V

STRUCTURE OF PLANT ORGANS

I. STRUCTURE OF STEMS

A. DICOTYLEDONOUS STEMS

1. STEM OF SUNFLOWER

A transverse section of a young stem of sunflower (*Helianthus annuus* of Fam. Compositae) shows the following arrangement of tissues (Figs. 231-233) from periphery towards the centre :

Epidermis. This is the outermost layer consisting of somewhat flattened cells, often containing chloroplasts, with their radial walls united closely to one another and with a distinct cuticle. This layer possesses stomata occasionally. Many multicellular hairs develop from epidermal cells.

Cortex. This tissue lies internal to epidermis and is differentiated into *three* distinct regions :

(a) *Hypodermis.* Towards the epidermis, a few layers of cells of the cortex become smaller and smaller, radially compressed, and having their cell walls thickened at the corners (collenchyma). The cells are living and contain a number of chloroplasts.

(b) *General cortex.* It is made up of large, more or less rounded, thin-walled parenchyma cells with conspicuous intercellular spaces. These cells gradually tend to become smaller towards the ring of vascular bundles, and ultimately, there is a layer forming a distinct uninterrupted sheet of closely fitting cells, which are always characterized by the presence of starch grains. This layer is, therefore, described as (c) the *starch sheath**.

*Occasionally, however, this layer does not contain starch grains, but undergoes a different type of development forming a typical endodermis, which is a constant feature in roots.

Here and there, in the general cortex, may be found secretory canals (ducts), each being surrounded by a ring of small cells with conspicuous protoplasmic contents.

Stele. All the tissues lying within the starch sheath together form the stele, which is differentiated into the following regions :

(a) *Pericycle.* It lies internal to the starch sheath and forms the outermost layer of the stele. It is composed of a few layers of cells, and is heterogeneous, *i.e.*, some of the cells are thin-walled

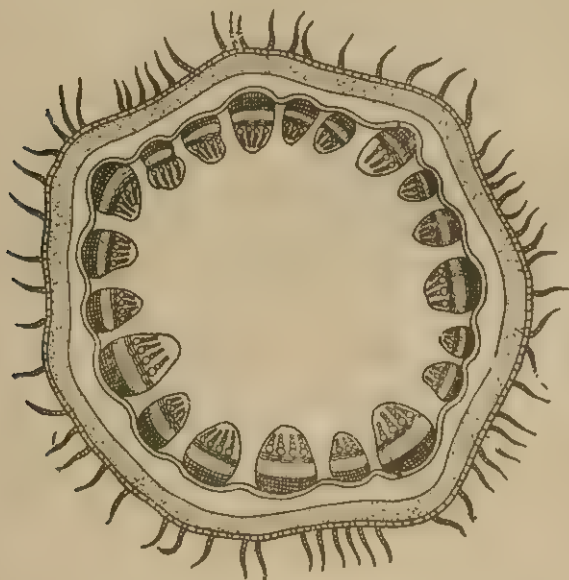


FIG. 231. T.S. OF SUNFLOWER STEM (*Diagrammatic*)

(parenchyma) and others thick-walled (sclerenchyma). These sclerenchymatous portions lie on the tops of vascular bundles forming the **bundle caps***.

(b) *Vascular bundles.* Within the pericycle the vascular bundles are found arranged in the form of a ring. Each vascular

*This bundle cap is a part of the vascular bundle and originates from the procambium strand. Since phloem is called soft bast, the term *hard bast* may be given to these groups of bast fibres.

bundle is conjoint, collateral and open. Lying internal to the bundle cap is the phloem consisting of sieve tubes, companion cells, and phloem parenchyma. Next to the phloem, there is a strip of tissue consisting of thin-walled, rectangular, meristematic

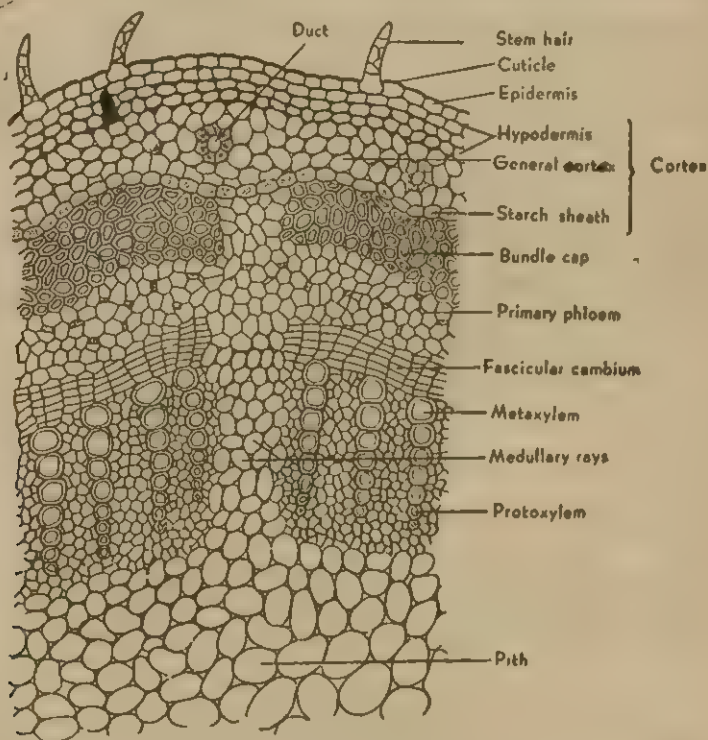


FIG. 232. T.S. OF SUNFLOWER STEM (in part)

cells, which divide by tangential divisions to form xylem and phloem. This tissue is the **cambium**. Internal to cambium lies the xylem. It is made up of protoxylem vessels (towards pith), metaxylem vessels (towards cambium), wood fibres and wood parenchyma.

(c) *Primary medullary rays*. These consist of thin-walled parenchyma cells and lie between two contiguous vascular bundles.

(d) *Pith*. It occupies the centre of the stem and is surround-

ed by the vascular bundles. The cells are thin-walled parenchyma, large, and with conspicuous intercellular spaces.

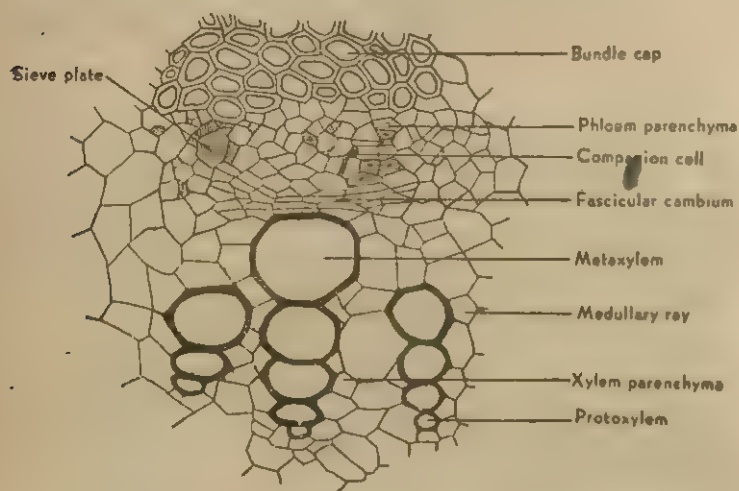


FIG. 233. A SINGLE BUNDLE FROM SUNFLOWER STEM

2. STEM OF CUCURBITA

A transverse section of a young stem of *Cucurbita* (Fam. Cucurbitaceae) shows the following arrangement of tissues (Figs. 234 & 235) from the periphery towards the centre :

Epidermis. It consists of one layer of cells with outer walls cuticularized, and with numerous multicellular hairs.

Cortex. It is comparatively thin and lies next to the epidermis and is composed of the following tissues :

(a) *Hypodermis.* It is composed of several layers of collenchyma cells, whose corners are thickened, but not lignified, and some of which may contain chloroplasts.

(b) *General cortex.* It consists of a few layers of thin-walled parenchyma cells, lying just internal to the hypodermis.

(c) *Starch sheath.* It is the innermost layer of the cortex,

consisting of a single layer of closely-packed barrel-shaped cells, without any intercellular space, and with abundant starch grains.

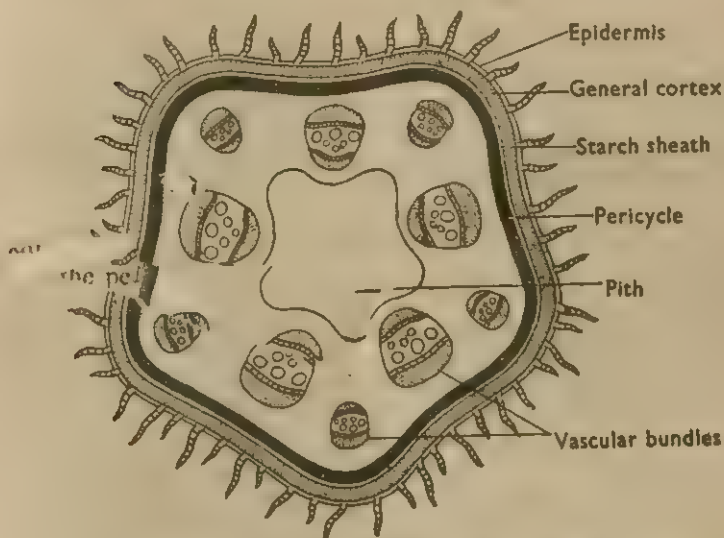


FIG. 234. T.S. OF *Cucurbita* STEM (Diagrammatic)

Stele. It is the central region of the stem, limited on the outer side by the starch sheath. It consists of the following tissues :

(a) *Pericycle.* It is composed of three to four layers of strongly thickened sclerenchyma cells, lying just internal to the starch sheath.

(b) *Ground tissue or Internal parenchyma.* It lies next to the pericycle and consists of several layers of thin-walled, large parenchyma cells, in which are embedded the vascular bundles.

(c) *Vascular bundles.* These are conjoint, bicollateral, open, usually ten in number and are arranged in two rings of five each,—a small outer bundle to each ridge, and a larger inner one to each furrow. Each vascular bundle, when examined from the periphery to the centre, shows the following tissues :

(i) *Outer phloem*. It consists of sieve tubes with conspicuous sieve plates, companion cells, and phloem parenchyma.

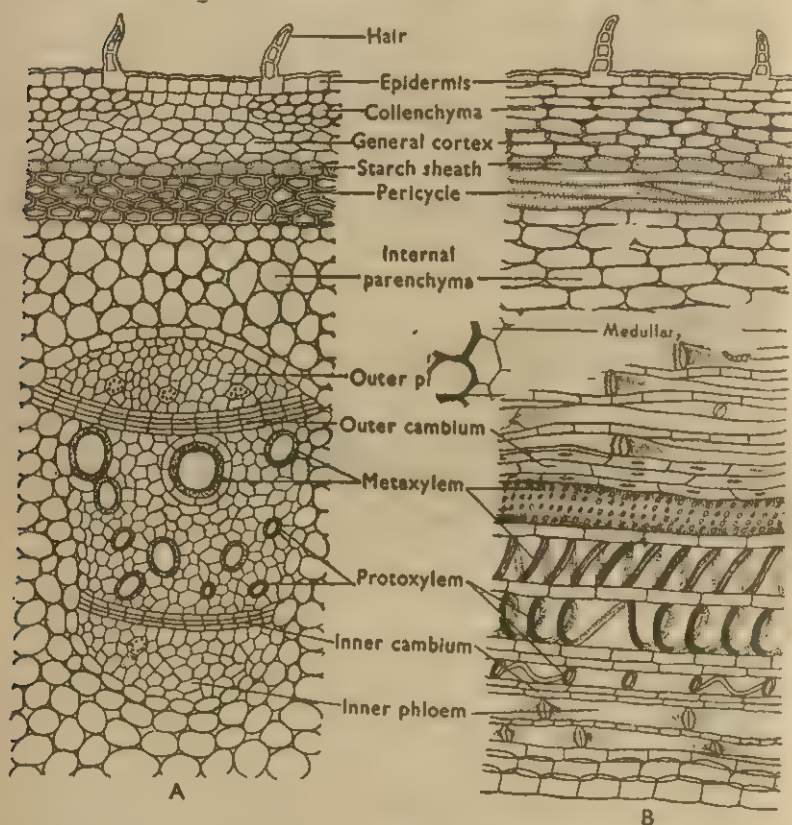


FIG. 235. T.S. (A) AND L.S. (B) OF *Cucurbita* STEM (in parts)

(ii) *Outer cambium*. It is composed of several layers of long narrow cells arranged in regular rows.

(iii) *Xylem*. It occupies the central portion of the vascular bundle and consists of two or three large pitted vessels (metaxylem) with wide cavities and many medium and small spiral and annular vessels (protoxylem). The rest of the xylem consists of wood parenchyma.

(iv) *Inner cambium*. It lies internal to xylem and consists of

a few layers of closely-packed, small cells. This tissue is incompletely developed.

(v) *Inner phloem*. It is similar in structure to the outer phloem.

(d) *Pith* is early disorganized, and the stem is hollow from the very early stage.

3. STEM OF LEONURUS

A transverse section of a young stem of *Leonurus* (Fam. Labiatae) shows the following arrangement of tissues (Fig. 236) from the periphery towards the centre :

Epidermis. It consists of a single layer of thin-walled cells with a thick sheet of cuticle on the outer surface. Numerous multicellular hairs are present.

Cortex. It is comparatively thin and lies next to the epidermis, and is composed of the following tissues :

(a) *Hypodermis*. It is made up of a few layers of collenchyma cells, which reach their maximum development at the four corners, but do not form continuous bands.

(b) *General cortex*. It consists of a few layers of thin-walled, isodiametric cells with intercellular spaces ; the cells contain abundant chloroplasts, hence the entire tissue appears as a green belt. It should be noted that where the hypodermis is discontinuous, this chlorophyllous tissue extends in an upward direction and occupies the position just beneath the epidermis.

(c) *Starch sheath*. It is a single wavy layer, composed of thin-walled, barrel-shaped cells with abundant starch grains.

Stele. It is the central region of the stem, limited on the outer side by the starch sheath. It consists of the following tissues :

(a) *Pericycle*. It is a few-layered sclerenchymatous tissue, forming a continuous band.

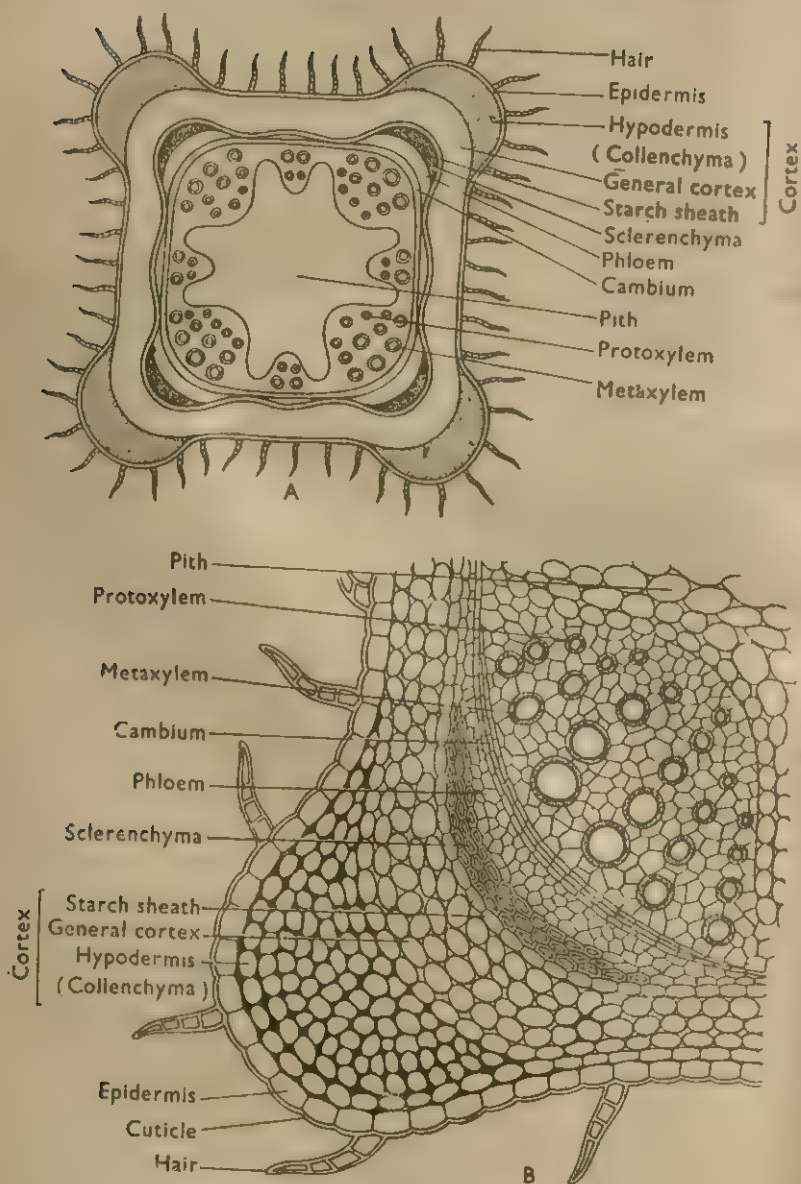


FIG. 236. T.S. OF *Leonurus* STEM

A, an entire section (diagrammatic); B, a portion of it (magnified).

(b) *Vascular bundles.* The vascular bundles occur closely towards the periphery ; they are conjoint, collateral and open. The phloem consists of sieve tubes, companion cells, and phloem parenchyma. Next to the phloem lies the cambium, composed of thin-walled rectangular cells. It is to be noted that the cambium ring is formed at an early stage. Internal to the cambium lies the xylem. It is composed of protoxylem and metaxylem vessels, wood fibres and xylem parenchyma.

(c) *Pith.* It occupies the centre of the stem, and is composed of large, oval or round parenchyma cells. Some of the cells lying in association with the vascular elements contain chloroplasts.

4. STEM OF CALOTROPIS

A transverse section of a young stem of *Calotropis* (Fam. Asclepiadaceae) shows the following arrangement of tissues (Fig. 237) from the periphery towards the centre :

Epidermis. It consists of a single layer of thin-walled tabular cells with a thick cuticle and a waxy coating. Stomata may be seen here and there.

Cortex. It is comparatively thin and lies next to the epidermis and is composed of the following structures :

(a) *Hypodermis.* It is made up of two or three layers of collenchyma.

(b) *General cortex.* It consists of a few layers of large parenchyma cells with intercellular spaces.

(c) *Starch sheath.* It is a single wavy layer, composed of compact, barrel-shaped cells containing abundant starch grains.

Stele. It is the central cylinder of the stem, limited on the outer side by the starch sheath. It is composed of the following tissues :

(a) *Pericycle.* It is few-layered and is composed of parenchyma cells having patches of phloem fibres here and there.

(b) *Vascular bundles*. The vascular bundles are conjoint, collateral and open. Phloem consists of sieve tubes, companion cells, and phloem parenchyma. Next to the phloem lies the cam-

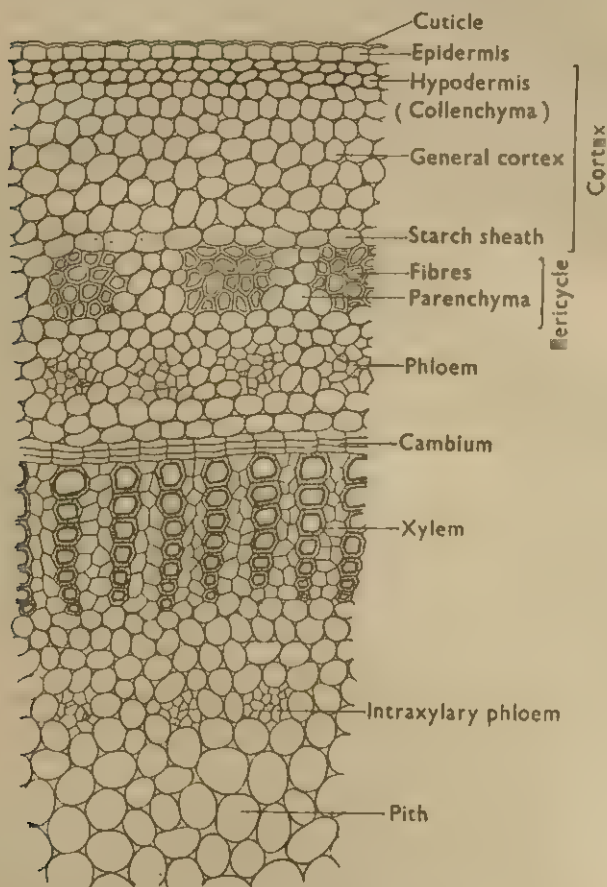


FIG. 237. T.S. OF *Calotropis* STEM (in part)

bium, composed of thin-walled, rectangular cells. Internal to cambium lies the xylem in the form of a cylinder. It is comparatively massive, and is composed of metaxylem and protoxylem. It is to be noted that below the xylem cylinder patches of intraxylary phloem are present.

(c) *Pith*. It occupies the centre of the stem and is composed of large, oval or round, parenchyma cells with conspicuous intercellular spaces.

5. STEM OF ENHYDRA

A transverse section of the stem of *Enhydra* (Fam. Compositae), an aquatic plant, shows the following arrangement of tissues (Fig. 238) from the periphery towards the centre :

Epidermis. This is the outermost layer consisting of cells with a thin layer of cuticle.

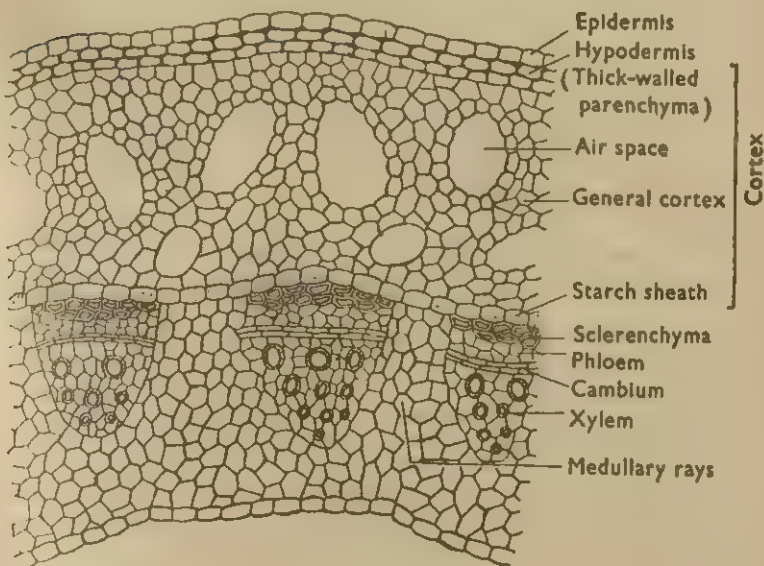


FIG. 238. T.S. OF *Enhydra* STEM (in part)

Cortex. It is comparatively thin and lies next to the epidermis, and is composed of the following tissues :

(a) *Hypodermis*. It is composed of two or three layers of comparatively thick-walled parenchyma cells.

(b) *General cortex*. It consists of several layers of thin-

walled parenchyma cells containing chloroplasts and provided with numerous large air spaces.

(c) *Starch sheath*. It is the innermost layer of the cortex and consists of a single wavy layer of thin-walled, compact cells containing starch grains.

Stele. It is the central region of the stem, limited on the outer side by the starch sheath. It consists of the following tissues :

(a) *Pericycle*. This tissue, like that of the sunflower stem, is a heterogeneous one, made up partly of parenchyma and partly of sclerenchyma, the latter forming a small bundle cap.

(b) *Vascular bundles*. These are not very well-developed, and are arranged in a ring. Each vascular bundle is conjoint, collateral and open.

(i) *Phloem*. It is comparatively small and consists of sieve tubes and companion cells.

(ii) *Cambium*. It is present as a thin layer between xylem and phloem, but in the older stem, it forms a continuous ring.

(iii) *Xylem*. It is also small in amount and consists of a few vessels and wood parenchyma.

(c) *Pith*. The cells of the pith are broken down leaving a big cavity at the centre.

(d) *Medullary rays*. These lie between two vascular bundles, and are composed of parenchyma cells.

B. MONOCOTYLEDONOUS STEMS

1. STEM OF MAIZE

A transverse section of the stem of maize (*Zea mays* of Fam. Gramineae) shows the following arrangement of tissues (Figs. 239-241) from the periphery towards the centre :

Epidermis. It forms the outermost layer consisting of somewhat flattened cells without any hair and with radial walls

closely united with one another. The outer free face of the cells is somewhat curved, strongly cutinized and with a thick cuticle. Here and there in the epidermis a few stomata may be seen.

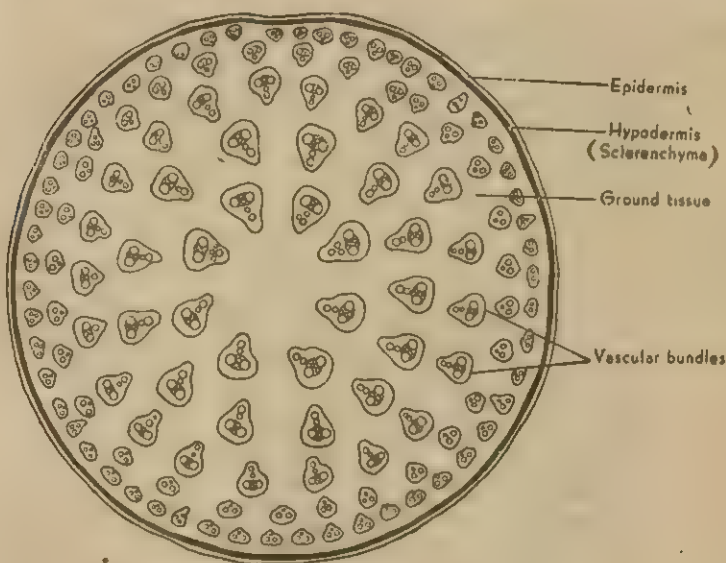


FIG. 239. T.S. OF MAIZE STEM (*Diagrammatic*)

Hypodermis. It lies internal to the epidermis and consists of one or two layers of thick-walled parenchyma cells. Internal to each stoma, the hypodermis is interrupted here and there by the underlying thin-walled parenchyma.

Ground tissue. It forms a continuous mass of thin-walled parenchyma cells with intercellular spaces and extending from below the hypodermis to the centre of the stem.

Vascular bundles. These are conjoint, collateral and closed. A large number of vascular bundles are scattered irregularly throughout the ground tissue, but becoming fewer and more and more isolated towards the centre. Towards the epidermis, they are very numerous, smaller and crowded, each being surrounded by a thick and conspicuous sheath of sclerenchyma (**bundle sheath**)

and often becoming continuous with the thick-walled hypodermis. In extreme cases, due to further development of thick-walled parenchyma between the hypodermis and the peripheral bundles,

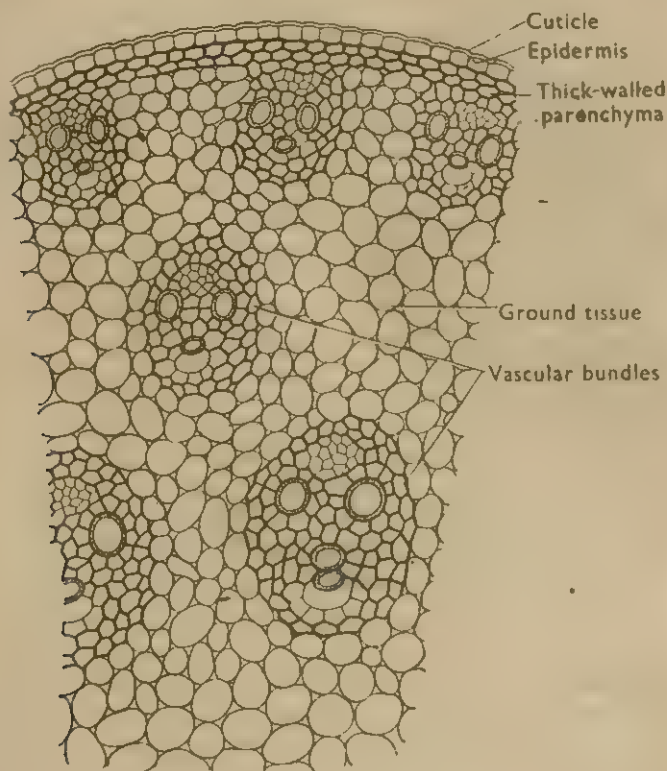


FIG. 240. T.S. OF MAIZE STEM (in part)

they appear to lie enclosed within it. Typically, each vascular bundle is very characteristic in having a sheath of sclerenchyma (sclerenchymatous bundle sheath) of its own.

The xylem usually consists of distinct vessels arranged in the form of the letter Y, the two arms of the Y are occupied by two big vessels (metaxylem—pitted) and the apex by smaller vessels (protoxylem—annular and spiral). On the inner side of the mature stem, the lowest protoxylem groups break down form-

ing a conspicuous cavity, known as the **protoxylem cavity**. On the outer face of the protoxylem are present a few lignified xylem elements, which are usually tracheids or small vessels.

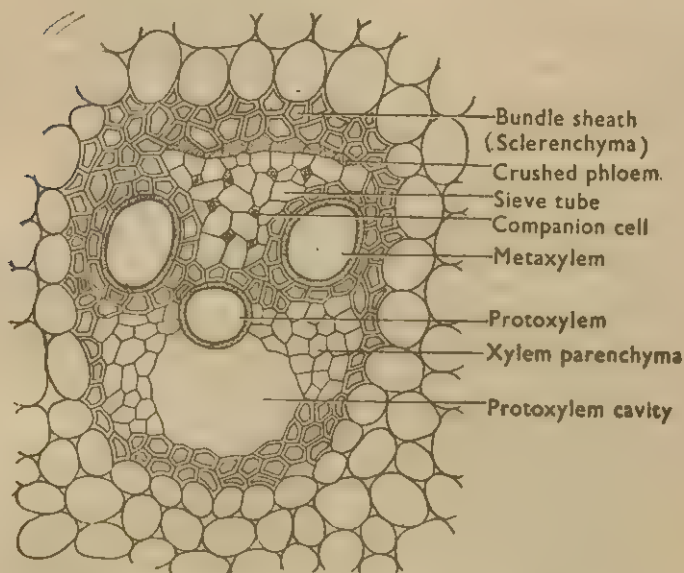


FIG. 241. A SINGLE VASCULAR BUNDLE FROM MAIZE STEM IN T.S.

The phloem consists exclusively of sieve tubes and companion cells, the phloem parenchyma being absent altogether. The primary protophloem is often crushed against the sclerenchymatous bundle sheath by the radial expansion of the later-formed metaphloem, and the former occupies the outermost portion and soon gets disorganized.

2. STEM OF ASPARAGUS

A transverse section of the stem of *Asparagus* (Fam. Liliaceae) shows the following arrangement of tissues (Fig. 242) from the periphery towards the centre :

Epidermis. It consists of a single layer of somewhat rounded cells with cuticle.

Ground tissue. It lies next to the epidermis and extends up to the centre of the stem. The outermost layers of the ground tissue are composed of parenchyma cells, of which the outer ones contain abundant chloroplasts but the inner ones are non-chlorophyllous. Next to the non-chlorophyllous tissue, there occurs a **perivascular strand** in the form of a band, which is composed of three layers of sclerenchyma. The central portion of the stem consists of thin-walled parenchyma cells with conspicuous intercellular spaces.

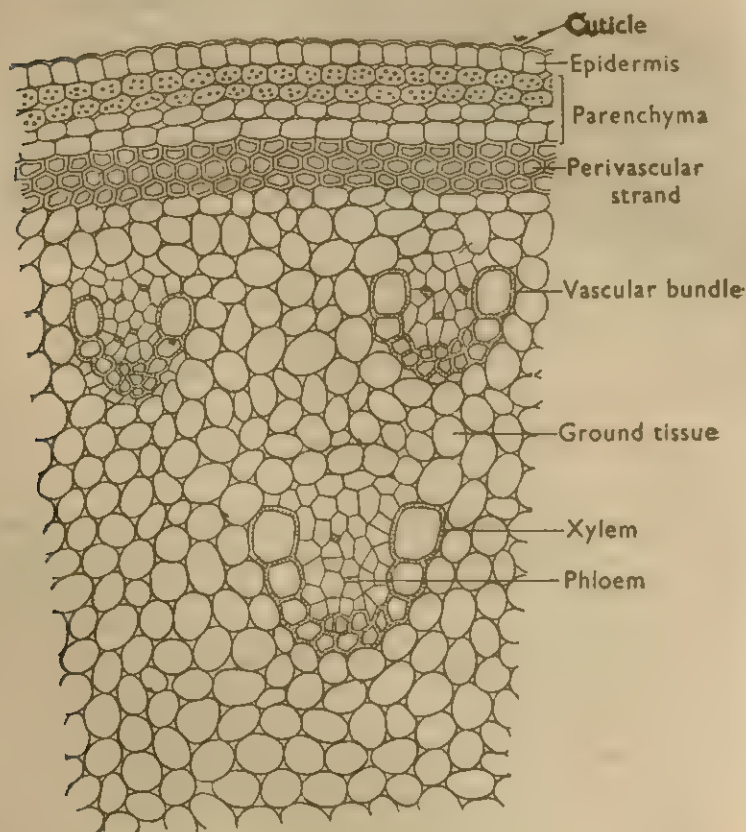


FIG. 242. T.S. OF *Asparagus* STEM (in part)

Vascular bundles. The vascular bundles are conjoint, collateral and closed, and are scattered in the ground tissue. The

vascular bundles situated towards the centre are larger than those towards the perivascular strand. In some cases, the peripheral vascular bundles may touch the perivascular strand. It is to be noted that the xylem is in the form of the letter V, protoxylem occupying the apex, and metaxylem, the two arms. The phloem is composed of sieve tubes and companion cells, and is situated between the two arms of V.

3. STEM OF *LEPTOCHLOA*

A transverse section of the stem of *Leptochloa* (Fam. Gramineae), an aquatic grass, shows the following arrangement of tissues (Fig. 243) from the periphery towards the centre :

Epidermis. It is the outermost portion and consists of a single layer of compact parenchyma cells with cuticularized outer walls.

Ground tissue. It extends from beneath the epidermis to the centre. The outermost layers are made up of two or three

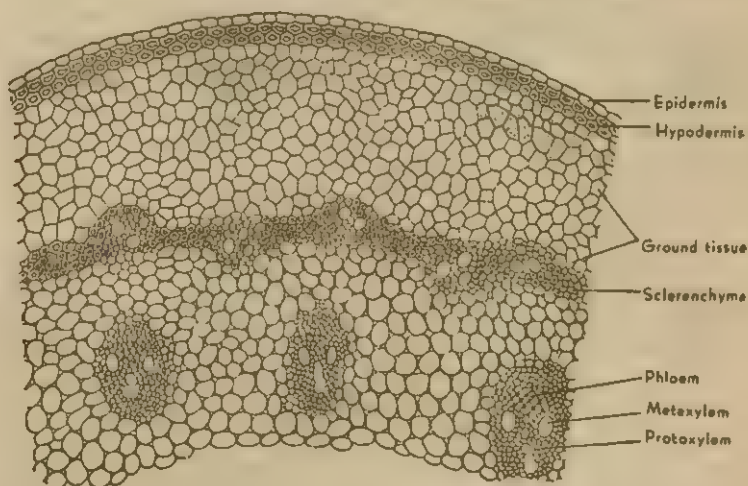


FIG. 243. T.S. OF *Leptochloa* STEM (in part)

layers of sclerenchyma cells ; this is the *hypodermis*. Next to the hypodermis, there are masses of parenchyma cells with prominent air spaces. Just below the parenchyma, one or two layers of sclerenchyma cells forming a band is present, to which a few

small vascular bundles are juxtaposed. The central portion is hollow.

Vascular bundles. These lie scattered in the ground tissue. Each bundle is collateral and closed, and is surrounded by a sclerenchyma sheath. The xylem consists of two pitted vessels (metaxylem) and one or two spiral and annular vessels (protoxylem). There is an air space below the annular vessel. The phloem consists of a few sieve tubes and companion cells.

4. SCAPE OF CANNA

A transverse section of the scape of *Canna* (S.F. Cannaceae) shows the following arrangement of tissues (Fig. 244) from the periphery towards the centre :

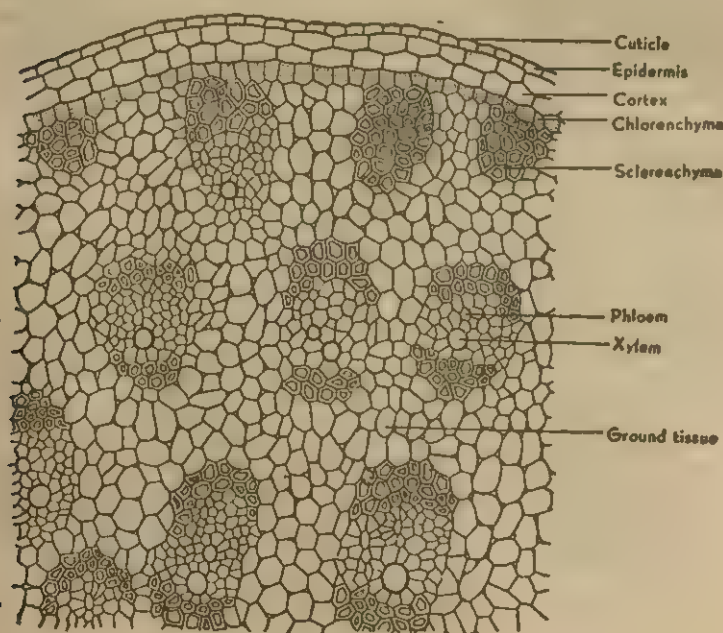


FIG. 244. T.S. OF *Canna* SCAPE (in part)

Epidermis. It forms the outermost layer consisting of a single layer of small tabular cells with cutinized outer walls.

Ground tissue. Lying within the epidermis, the whole mass of tissues, excepting the vascular bundles, forms the ground tissue system. It can be differentiated into :

(a) *cortex*, consisting of two layers of thin-walled parenchyma and lying just internal to the epidermis ;

(b) *chlorophyllous tissue*, usually consisting of a single layer of chloroplast-containing parenchyma cells internal to the cortex ;

(c) *sclerenchyma*, forming isolated patches and in contact with the chlorophyllous tissue ; and

(d) *ground tissue*, consisting of typical parenchyma and forming the main bulk of the scape, in which the vascular bundles are scattered.

Vascular bundles. These lie scattered in the ground tissue, and are of various sizes. Each bundle is conjoint, collateral and closed, and consists of xylem on the inner side and phloem on the outer one. The sclerenchymatous bundle sheath is usually not continuous, but it occurs in the form of two separate patches, one on the outer side forming a cap, and the other on the inner side as a somewhat narrow strip.

The main differences between the primary structures of dicotyledonous and monocotyledonous stems may be tabulated as follows :

| <i>Dicotyledonous stem</i> | <i>Monocotyledonous stem</i> |
|---|--|
| 1. The ground tissue is differentiated into extra-stelar and intra-stelar regions, limited internally by the starch sheath. | 1. There is usually no differentiation of the ground tissue into extra-stelar and intra-stelar regions, but it extends from beneath the hypodermis right up to the centre. |
| 2. The hypodermis is made up of collenchyma. | 2. The hypodermis is usually made up of thick-walled parenchyma. |
| 3. Vascular bundles are less in number and are arranged in the form of a ring. | 3. Vascular bundles are numerous and lie scattered in the ground tissue. |
| 4. Each vascular bundle is open and either collateral or bicollateral. Phloem parenchyma is usually present. | 4. Each vascular bundle is normally closed and usually collateral. Phloem parenchyma is absent. |
| 5. Bundles are not surrounded by a sclerenchymatous sheath. | 5. Each bundle is generally surrounded by a sclerenchymatous sheath. |

Dicotyledonous stem

6. Vascular bundles are wedge-shaped.

Monocotyledonous stem

6. Vascular bundles are oval. The xylem vessels are arranged in a more or less Y- or V-shaped manner; the two big pitted vessels (metaxylem) occupy the two arms, and the apex of Y or V is occupied by annular and spiral vessels and a large protoxylem cavity, in some cases. The phloem lies towards the outside but between the two arms of Y or V.

II. STRUCTURE OF ROOTS

A. DICOTYLEDONOUS ROOTS

1. ROOT OF GRAM

A transverse section of a young root of gram (*Cicer arietinum*) of S.F. Papilionaceae (Fam. Leguminosae) shows the following arrangement of tissues (Fig. 245) from the periphery towards the centre :

Epiblema or piliferous layer. This is the single outermost layer of living cells, which are characterized by the lack of cuticle and the presence of unicellular root hairs, which are nothing but some of its cells elongated.

Cortex. It lies internal to the epiblema and consists of a comparatively thick band of unspecialized large, living parenchyma cells with many intercellular spaces. These cells often contain leucoplasts and starch grains.

The cortex is delimited from the stele by a single layer of well-defined, barrel-shaped cells without intercellular spaces forming the *endodermis*. The radial walls of each cell have peculiar thickenings which lie in the form of a band running completely round the inner surface of the radial walls; this band is termed the *casparian strip*. It appears lenticular in transverse section.

Stele. Lying enclosed by the endodermis is the stele, which is differentiated into the following regions :

(a) *Pericycle.* It is the outermost layer of the stele consisting of a single layer of thin-walled parenchyma cells.

(b) *Vascular bundles.* The vascular bundles are of the radial type; here xylem and phloem are equal in number, alter-

nate with one another and are arranged in the form of a ring. The number of xylem or phloem is four, *i.e.*, **tetrarch**. The protoxylem lies towards the periphery and the metaxylem towards the centre, so the arrangement is **exarch**. The phloem

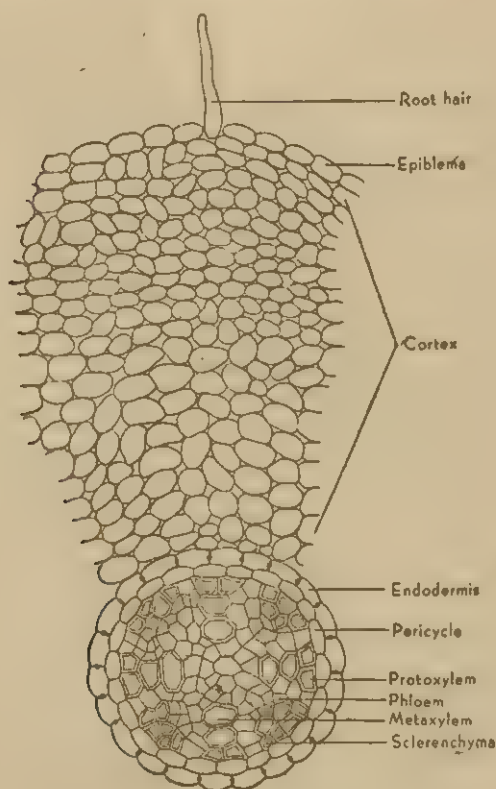


FIG. 245. T.S. OF GRAM ROOT (*in part*)

bundles consist of sieve tubes, companion cells and phloem parenchyma. Opposite each phloem bundle, towards the pericycle, there is a group of sclerenchyma fibres.

(c) *Pith*. Pith is absent in the gram root.*

*The so-called 'pith', which is sometimes present, is nothing but undifferentiated xylem; during later stages, the central position is occupied by xylem alone.

2. ROOT OF PEA

A transverse section of a young root of pea (*Pisum sativum*) of S.F. Papilionaceae (Fam. Leguminosae) shows the following

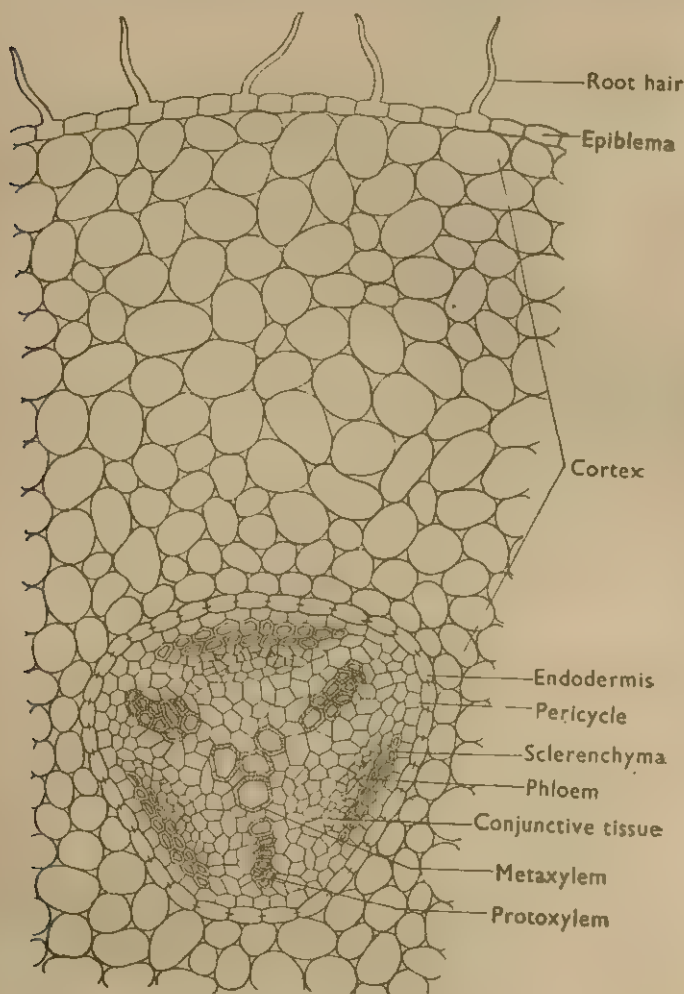


FIG. 246. T.S. OF PEA ROOT (*in part*)

arrangement of tissues (Fig. 246) from periphery towards the centre :

Epiblema or piliferous layer. It consists of a single layer of thin-walled cells, some of which are prolonged into unicellular root hairs.

Cortex. It lies internal to epiblema, and is composed of many layers of thin-walled parenchyma cells with conspicuous intercellular spaces.

The innermost layer of the cortex is called the *endodermis*. It is single-layered, and composed of barrel-shaped cells without any intercellular spaces, and provided with casparian strips.

Stele. It lies internal to the endodermis and is differentiated into the following regions :

(a) *Pericycle.* It is the outermost layer of the stele consisting of a single layer of thin-walled parenchyma cells.

(b) *Vascular bundles.* The vascular bundles are radial. Here, they are **triarch**, i.e., three patches of xylem are alternating with three patches of phloem. Xylem is typically *exarch* having protoxylem towards the periphery and metaxylem towards the centre. The phloem is comparatively small and consists of sieve tubes, companion cells and phloem parenchyma. Opposite each phloem bundle, towards the periphery, there is a group of sclerenchyma fibres.

(c) *Conjunctive tissues.* The conjunctive tissues lie between xylem and phloem groups, and are composed of parenchyma cells.

(d) *Pith.* A very small pith is present in the early stage, but it is obliterated afterwards.

3. ROOT OF CUCURBITA

The structure of the root of *Cucurbita* of Fam. Cucurbitaceae (Fig. 247) is almost similar to that of the gram root, exceptions being the absence of sclerenchyma fibres below the phloem bundles and the presence of a well-differentiated pith.

B. MONOCOTYLEDONOUS ROOTS

1. ROOT OF CANNA

A transverse section of the root of *Canna* (Fam. Cannaceae) shows the following arrangement of tissues (Fig. 248) from the periphery towards the centre :

✓ **Epiblema or piliferous layer.** This is the outermost layer of living cells, which are characterized by the lack of cuticle and the presence of unicellular root hairs, which are nothing but some of its cells enlarged.*

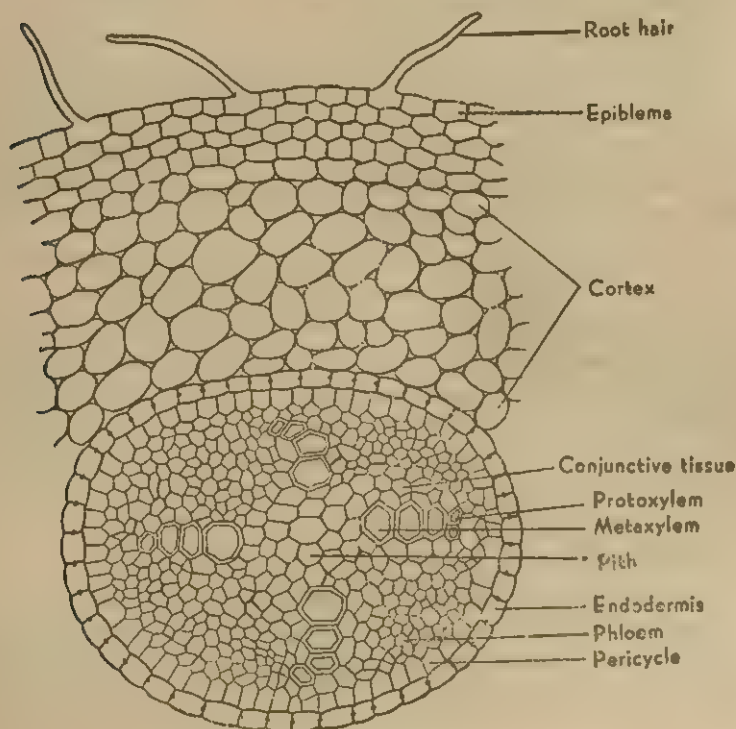


FIG. 247. T.S. OF *Cucurbita* ROOT (in part)

Cortex. It lies internal to the epiblema and consists of a comparatively thick band of unspecialized large, living, parenchyma cells with much intercellular spaces. These cells often contain starch grains and leucoplasts.

The cortex is delimited from the stele by a single layer of well-defined, barrel-shaped cells without intercellular spaces, forming the *endodermis*. Here the radial walls are provided with casparian strips, and the inner walls are also thickened with

*When the root hairs cease to function and wither away, the piliferous layer and often a few outer layers of the cortex become suberized and form a dead tissue, called the *exodermis*, well adapted as a protective coat.

the exception of the **passage cells**, which lie opposite to the protoxylem groups of the vascular bundles.

Stele. Enclosed by the endodermis is the stele, which is differentiated into the following regions :

(a) *Pericycle.* It is the outermost layer of the stele consisting of a single layer of thin-walled parenchyma cells.

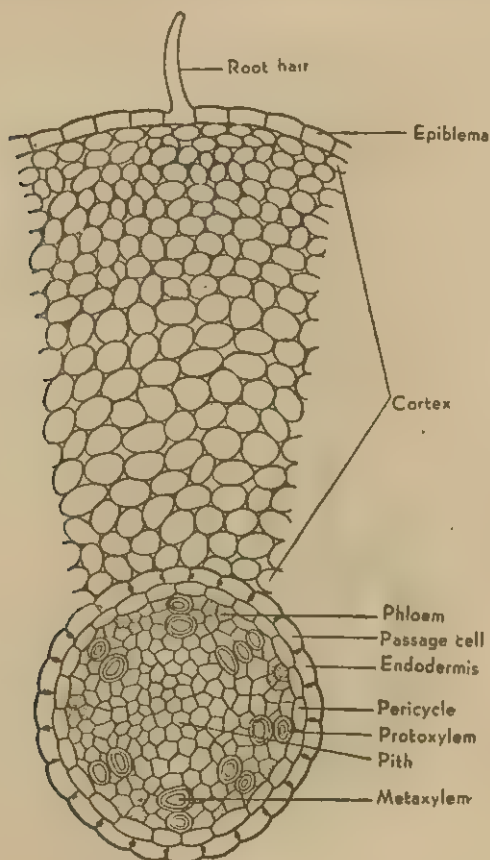


FIG. 248. T.S. OF *Canna* ROOT (In part)

(b) *Vascular bundles.* These are of the radial type. The number of xylem or phloem bundles is numerous, *i.e.*, **polyarch**. In other respects, the bundles are similar to those of the dicotyledonous roots.

(c) *Pith*. There is a well-differentiated pith at the centre consisting of thin-walled parenchyma cells.

2. ROOT OF MAIZE

The structure of the root of maize (*Zea mays*) of Fam. Gramineae (Fig. 249) is almost similar to that of *Canna*.*

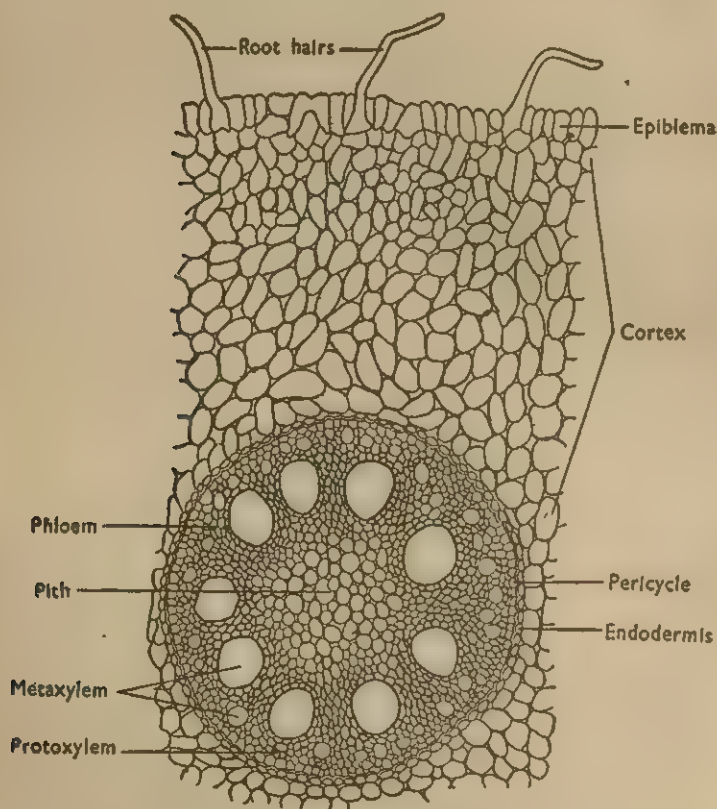


FIG. 249. T.S. OF MAIZE ROOT (*in part*)

3. AERIAL ROOT OF VANDA

A transverse section of the aerial root of *Vanda* (Fam.

*In the underground roots of monocots (e.g., *Canna*, maize, etc.), the pith is sclerified or mixed, while, in the aerial roots, it is usually parenchymatous, but the hypodermal region is more or less sclerified.

Orchidaceae) shows following arrangement of tissues (Fig. 250) from the periphery towards the centre :

Velamen. It consists of a few layers of thin-walled, elongated cells. The outermost layer is known as the **limiting layer**.

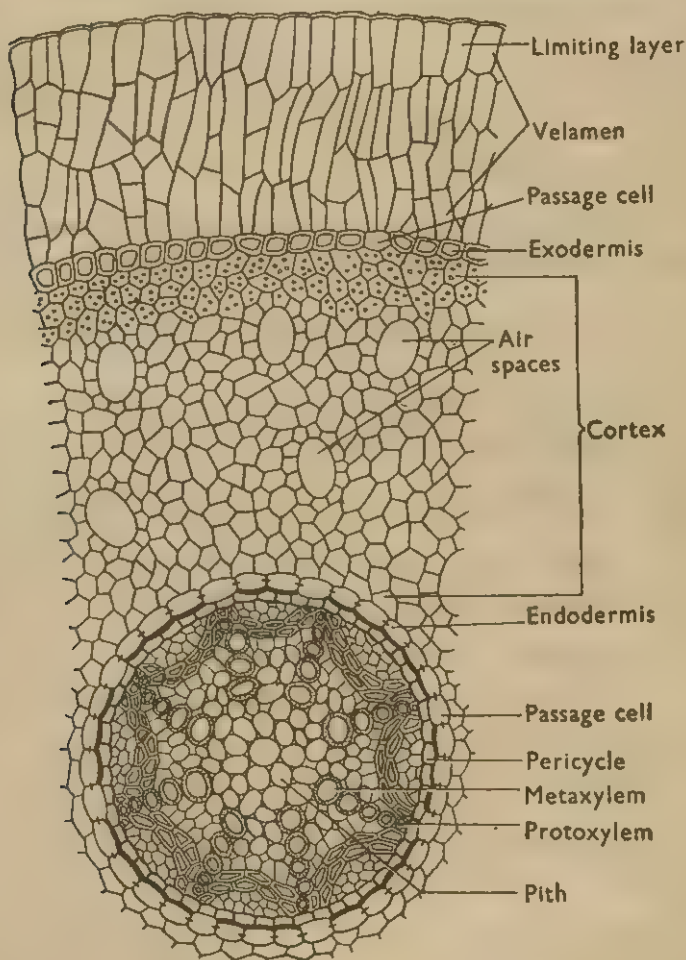


FIG. 250. T.S. OF ROOT OF *Vanda* (in part)

Exodermis. It consists of a single layer of thick-walled cells interrupted by thin-walled cells, known as **passage cells**. The

passage cells act as channels for the inward conduction of water absorbed by the velamen.

Cortex. It consists of many layers of thin-walled, oval or rounded, parenchyma cells with prominent air spaces. The outer layer contains chloroplasts.

Endodermis. It is composed of a single layer of cells with suberized radial and inner walls, and is interrupted by thin-walled cells, the so-called '*passage cells*'. These passage cells lie opposite to the protoxylem vessels.

Stele. Lying enclosed by the endodermis is the stele, which is differentiated into the following regions :

(a) *Pericycle.* It consists of a single layer of thin-walled cells.

(b) *Vascular bundles.* There are several bundles of xylem and phloem situated in different radii.

(c) *Conjunctive tissue.* The cells of this tissue are sclerenchymatous and partially surround the phloem groups.

(d) *Pith.* It consists of a mass of thin-walled parenchyma cells occupying the centre. Ducts are often present.

4. BREATHING ROOT OF *CERIOPS*

A transverse section of the breathing root of *Ceriops* (Fam. Rhizophoraceae) shows the following arrangement of tissues (Fig. 251) from the periphery towards the centre :

Cork. It is the outermost layer, and is composed of a few suberized cells with small lenticels here and there.

Cortex. The cortex is thick and spongy in nature, and is made up of several layers of thin-walled, roundish to polygonal cells with prominent air spaces.

Endodermis. It is a single-layered structure consisting of barrel-shaped cells, and is circular in outline.

Stele. Lying enclosed by the endodermis is the stele, which is differentiated into the following regions :

(a) *Pericycle.* It is few-layered, the outermost of which is parenchymatous, while the inner ones are sclerenchymatous.

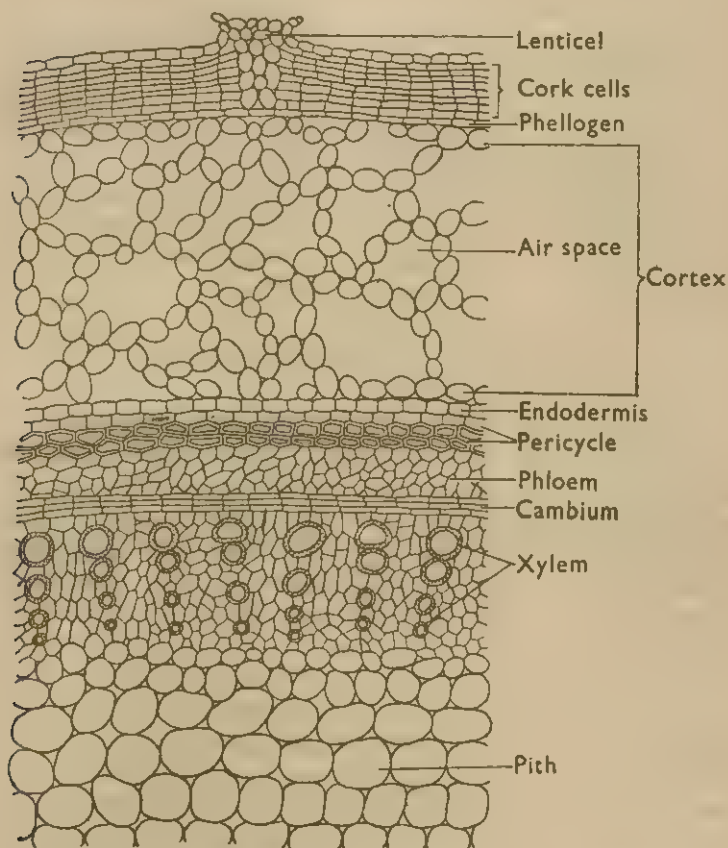


FIG. 251. T.S. OF BREATHING ROOT OF *Ceriops* (tn part)

(b) *Vascular bundles.* The vascular bundles form a continuous cylinder, and, like those of dicotyledonous stems, they are conjoint, collateral and open ; the xylem is endarch.

(c) *Pith.* It is composed of a mass of thin-walled parenchyma cells.

The main differences between the primary structures of dicotyledonous and monocotyledonous roots may be tabulated as follows :

| <i>Dicotyledonous root</i> | <i>Monocotyledonous root</i> |
|---|--|
| 1. A distinct endodermis is present, whose radial walls are thickened by casparian strips. | 1. A distinct endodermis with casparian strip is present ; outer and inner walls of the endodermal cells are also thickened with the exception of passage cells. |
| 2. Vascular bundles are radial, and the number of xylem and phloem bundles usually varies from two to five, rarely greater. | 2. Vascular bundles are radial, and the number of xylem and phloem bundles is usually numerous, rarely less. |
| 3. Pith may or may not be present. | 3. A conspicuous pith is invariably present. |

ROOT-STEM TRANSITION (Fig. 252)

Although the vascular bundles are continuous throughout root and stem, one notices differently constructed vascular bundles in the two cases. The change from the radial type of the vascular structure of the root to the conjoint and collateral type of the stem takes place in a part of the axis of the seedling, called the **transition region**. This transition may occur at the top of the radicle near the very base of the hypocotyl, near its centre, or in its upper part. The most essential fact of transition is that each strand of xylem of the root rotates through 180° round its longitudinal axis. This takes place in different ways, of which *four* main types may be distinguished : (1) Each xylem strand forks by a radial division. The branches, one to the right and one to the left, turn through 180° and join the phloem strand on the inside (Fig. 252, A). In this type, there are found in the stem as many primary bundles as there are phloem strands in the root, e.g., *Mirabilis* (Fam. Nyctaginaceae). (2) In this type, the strands of phloem as well as those of xylem fork. The branches of each swing laterally as they pass upwards, the xylem strands becoming inverted as before, but the phloem strands retaining their original orientation (Fig. 252, B). There are, thus, found in the stem twice as many bundles as there are phloem strands in the root, e.g., *Cucurbita* (Fam. Cucurbitaceae), *Tropaeolum*, (Fam. Tropaeolaceae), etc. (3) The

xylem strands do not divide, but continue their direct course in the stem twisting through 180° . Meanwhile, the phloem strands divide and the halves swing laterally to the position of the xylem, joining the xylem strands on the outside (Fig. 252, C), e.g., *Phoenix* (Fam. Palmae), *Lathyrus* and *Medicago* (S.F. Papilionaceae of

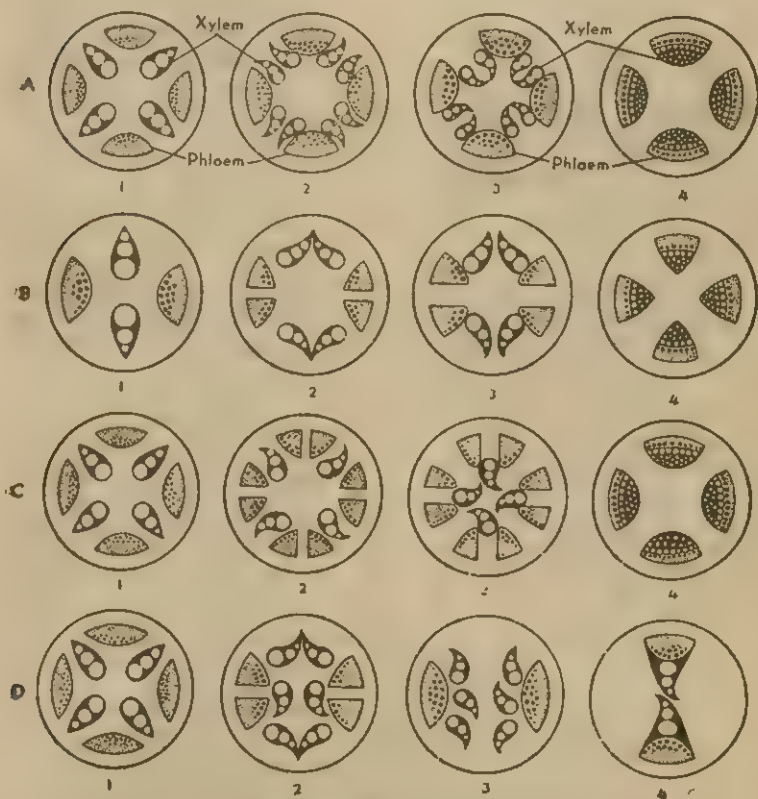


FIG. 252. DIFFERENT TYPES OF ROOT-STEM TRANSITION
(Modified after Holman & Robbins, and Eames & MacDaniels).

Fam. Leguminosae), etc. (4) In this type, the phloem strands remain as usual and do not undergo any division, while half of the xylem strands divide, the other half remaining unforked but getting inverted. The branches then swing laterally and join up with these unforked strands (Fig. 252, D). This type is rather rare and is found only in some monocotyledonous plants.

ORIGIN OF LATERAL ROOT (Fig. 253)

Lateral roots are commonly formed in acropetal order of succession in the region just behind the zone of root hairs. The

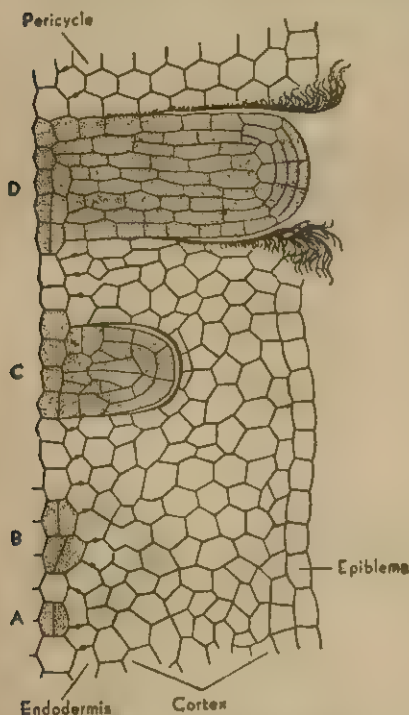


FIG. 253. STAGES IN THE DEVELOPMENT OF LATERAL ROOT
(Modified after Holman & Robbins).

origin of lateral root is endogenous, since in spermatophyta the meristem arises in the pericycle, and in pteridophyta it originates in the endodermis. A few parenchymatous cells begin to divide and become meristematic. A definite growing point is formed with its initial cells, the root cap and other characteristics. The lateral roots then break through the cortex during their emergence in order of development from the main root. In spermatophyta, the points of origin of lateral roots are opposite to the xylem rays, where there are more than two such strands; in pteridophyta, these are, in all cases, opposite to the xylem strands. Owing to this fixed position of

lateral root formation, there appear in vertical rows as many lateral roots as there are rays of xylem.

III. STRUCTURE OF LEAVES

A. DICOTYLEDONOUS LEAVES

1. LEAF OF MANGO

A transverse section of the leaf of mango (*Mangifera indica*) of Fam. Anacardiaceae at right angles to one of the veins shows

the following structure (Fig. 254) when observed under the microscope :

Upper epidermis. It consists of a single layer of closely fitting cells, with outer walls thickened, cutinized and cuticularized. It usually does not contain chloroplasts and stomata.

Mesophyll. It consists of a parenchyma tissue differentiated into two regions :

(a) *Palisade parenchyma.* It consists of two layers of closely packed columnar cells, each containing a large number of chloroplasts, which generally line the radial walls.

(b) *Spongy parenchyma.* It consists of a number of loosely packed parenchyma cells, more or less irregular in outline, with large intercellular spaces among them. These cells contain a fewer number of chloroplasts. Some of the spongy cells are seen to be united with one or more palisade cells, and these are called the **collecting cells**.

Vascular bundles. These are found in large numbers in the spongy tissue. Each bundle is surrounded by a sheath of parenchyma, known as the **bundle sheath**. The bundle is conjoint, collateral and closed, with the xylem disposed towards the upper epidermis and the phloem towards the lower one.

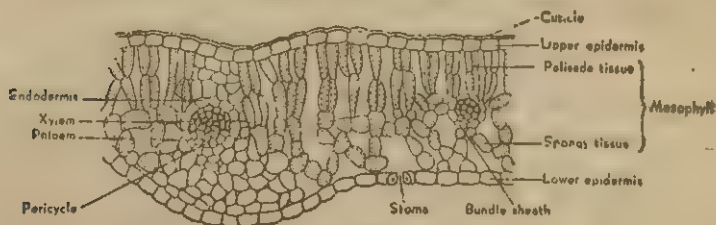


FIG. 254. T.S. OF MANGO LEAF (in part)

The xylem consists of annular and spiral vessels, tracheids, wood fibres and xylem parenchyma. The phloem consists of narrow sieve tubes, companion cells and phloem parenchyma.

Lower epidermis. It is like the upper one consisting of a single layer of cells, but differing from it in having numerous

stomata. Each stoma is provided with a respiratory cavity behind it, and is surrounded by two guard cells, containing green plastids and starch grains.

2. LEAF OF INDIA RUBBER

The structure of the leaf of the India rubber plant (*Ficus elastica*) of Fam. Moraceae is almost similar to that of the

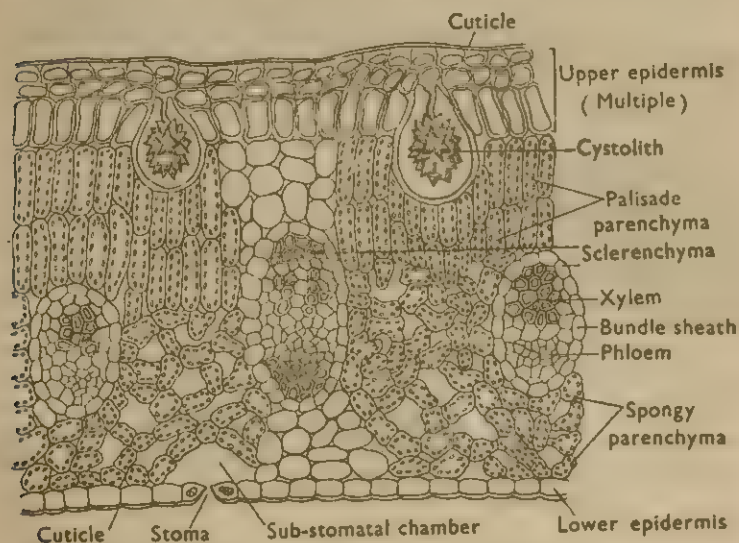


FIG. 255. T.S. OF INDIA RUBBER LEAF (in part)

mango, but the upper epidermis is multiple and some of its large inner cells (lithocysts) contain cystoliths (Fig. 255).

3. LEAF OF OLEANDER

A transverse section of the leaf of oleander (*Nerium peruvianum* = *N. odorum*) of Fam. Apocynaceae, a xerophytic plant, shows the following structure (Fig. 256) when observed under the microscope :

Upper epidermis. It consists of a few layers of parenchyma cells without intercellular spaces, and is provided with a thick cuticle on the outer surface. Numerous uniseriate multicellular hairs are present.

Mesophyll. It is clearly differentiated into palisade and spongy parenchymas, the former occurring both towards the upper epidermis and the lower one, while the latter lies in between them.

(a) *Upper palisade parenchyma*, consisting of three or more layers of closely packed, radially elongated parenchyma cells, containing numerous chloroplasts. The intercellular spaces are practically absent.

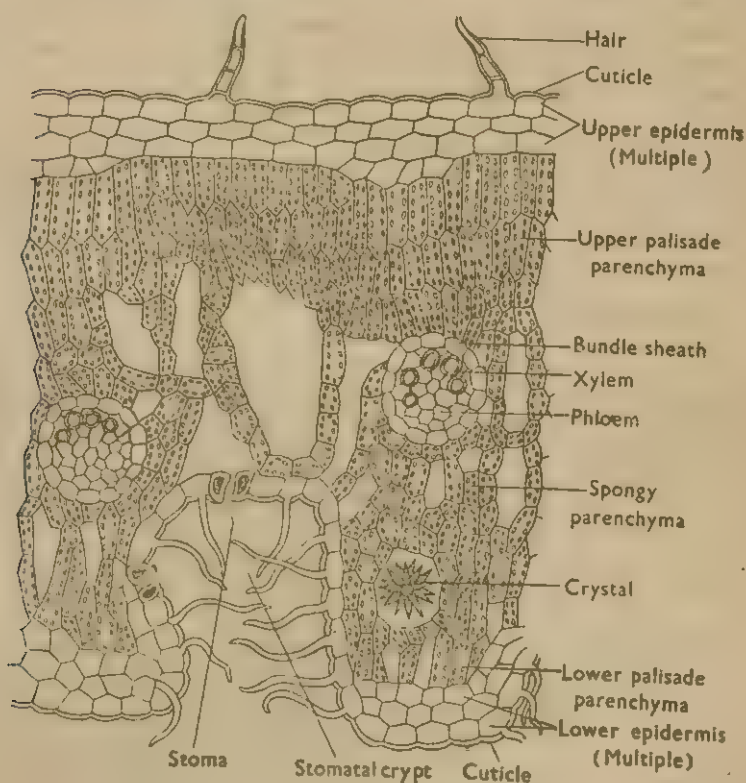


FIG. 256. T.S. OF OLEANDER LEAF (in part)

(b) *Spongy parenchyma*, composed of a few layers of loosely arranged, thin-walled, isodiametric cells containing a few chloroplasts. The intercellular spaces are abundant. Some of the cells contain aggregates of calcium oxalate crystals.

(c) *Lower palisade parenchyma*, situated below the spongy

parenchyma, usually consisting of a single or more layers of palisade cells.

Vascular bundles. These lie between the upper palisade and spongy parenchymas with the xylem facing upwards and the phloem downwards. Each bundle is surrounded by a parenchymatous bundle sheath.

Lower epidermis. It is also few-layered like the upper epidermis, and is provided with a comparatively thinner cuticle. Stomata are sunken in crypts. There are numerous trichomes developed from the cells bordering the crypts.

4. LEAF OF LIMNANTHEMUM

A transverse section of the leaf of *Limnanthemum* (Fam. Gentianaceae), an aquatic plant, shows the following structure (Fig. 257) when observed under the microscope :

Upper epidermis. It is one-layered and is composed of closely

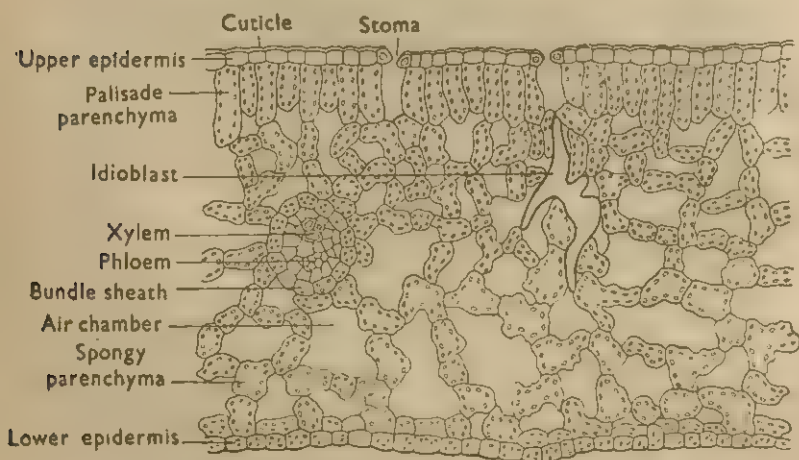


FIG. 257. T.S. OF *Limnanthemum* LEAF (in part)

packed parenchyma cells, whose outer walls are cuticularized. Stomata are present.

Mesophyll. This tissue is differentiated into palisade and spongy parenchymas.

(a) *Palisade parenchyma* is situated towards the upper epidermis and at right angles to it. The cells are columnar and closely packed, and contain numerous chloroplasts.

(b) *Spongy parenchyma* is situated towards the lower epidermis. The cells are polygonal and loosely arranged, so that numerous air spaces are present. They contain less chloroplasts. Idioblasts are frequently present in the air chambers.

Vascular bundles are poorly developed. Each bundle is conjoint, collateral and closed, and is surrounded by a chlorophyllous bundle sheath.

Lower epidermis. It is also one-layered and consists of parenchyma cells. The cells contain chloroplasts. The cuticle is very thin. Stomata are absent.

B. MONOCOTYLEDONOUS LEAVES

1. LEAF OF MAIZE

A transverse section through a leaf of maize (*Zea mays*) of Fam. Gramineae shows the following structure (Fig. 258) when observed under the microscope :

Upper epidermis. It consists of a single layer of non-chlorophyllous cells with numerous stomata. Bulliform cells are present.

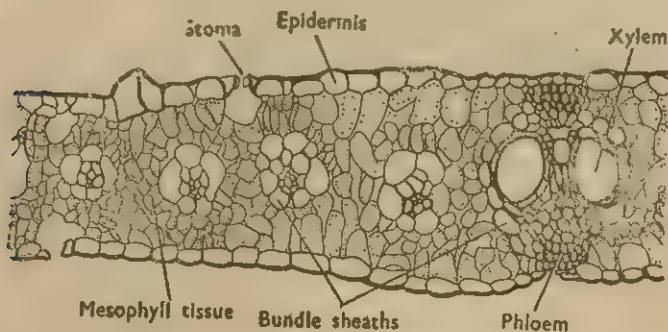


FIG. 258. T.S. OF MAIZE LEAF (in part)

Mesophyll. This tissue constitutes the main bulk of the leaf and lies in between the two layers of epidermis. The cells

are relatively compact with numerous chloroplasts, with a few intercellular spaces, and there is no differentiation into palisade and spongy parenchymas.

Vascular bundles. These are collateral and are of two types. The large bundles resemble the vascular bundles of the stem, but the mechanical tissue of the bundle sheath here forms two isolated patches of thick-walled elements, above and below each bundle. Besides, the xylem and phloem are surrounded by a sheath of chlorophyllose cells. The bundles are so oriented that the xylem lies towards the upper epidermis. The smaller bundles are similar in structure but without the adjacent mechanical tissues.

Lower epidermis. It is similar to the upper epidermis and contains numerous stomata.

2. LEAF OF TUBEROSE

A transverse section of the leaf of tuberose (*Polianthes tuberosa*) of Fam. Amaryllidaceae shows the following structure (Fig. 259) when observed under the microscope :

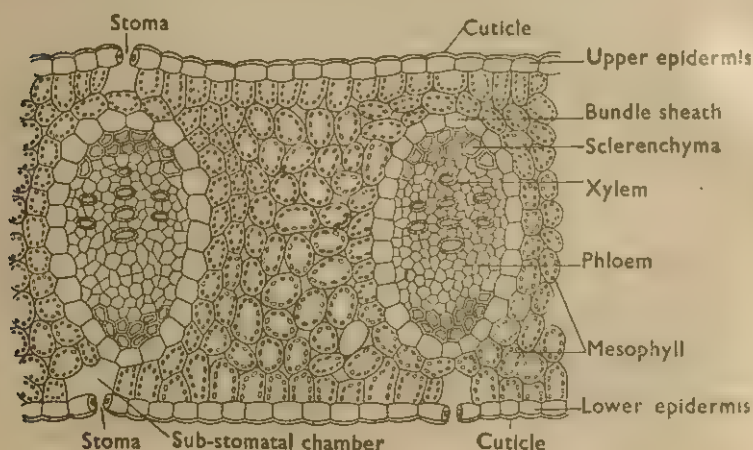


FIG. 259. T.S. OF TUBEROSE LEAF (in part)

Upper epidermis. It is one-layered and consists of compact rectangular cells with a thick layer of cuticle on the outer face. Stomata are present here and there.

Mesophyll. This tissue is not differentiated into palisade and spongy parenchymas. The cells are more or less isodiametric and contain numerous chloroplasts. Intercellular spaces are present.

Vascular bundles. The bundles are arranged in parallel series. Each bundle is conjoint, collateral and closed, and is surrounded by a parenchymatous bundle sheath. A few sclerenchyma cells occur at the upper and lower ends of each bundle.

Lower epidermis. It is similar to the upper epidermis.

3. LEAF OF BANANA

A transverse section of the leaf of banana (*Musa paradisiaca* var. *sapientum*) of Fam. Musaceae shows the following structure (Fig. 260) when observed under the microscope :

Upper epidermis. It consists of one layer of parenchyma cells with outer walls cutinized. Stomata may be present.

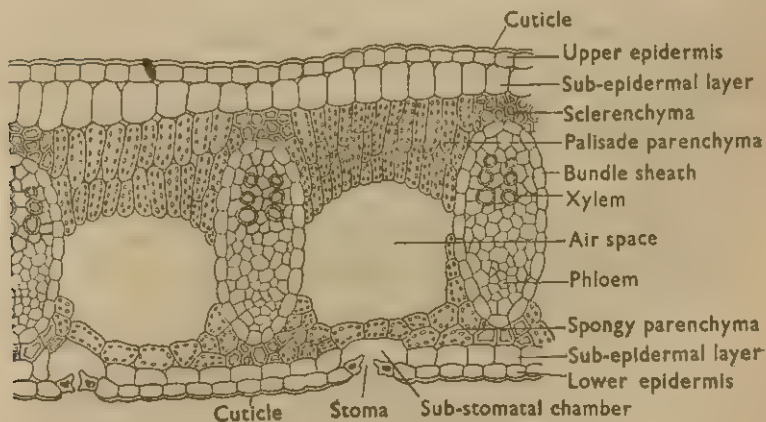


FIG. 260. T.S. OF BANANA LEAF (in part)

Sub-epidermal layer. It lies next to the epidermis and consists of a single layer of large thin-walled cells.

Mesophyll. It is differentiated into palisade and spongy parenchymas.

(a) *Palisade parenchyma.* It consists of two or three layers

of closely packed columnar cells with numerous chloroplasts and intercellular spaces.

(b) *Spongy parenchyma*. It consists of a few layers of small, nearly isodiametric cells with large, parallel-running air chambers at regular intervals.

Vascular bundles. These are poorly developed. Each bundle is closed. Patches of sclerenchyma occur on the upper and lower sides of the bundles.

Lower epidermis. It consists of one layer of roundish cells with cutinized outer walls. Slightly sunken stomata are present here and there.

4. LEAF OF BAMBOO

A transverse section of the leaf of bamboo (*Bambusa arundinacea*) of Fam. Gramineae shows the following structure (Fig. 261) when observed under the microscope :

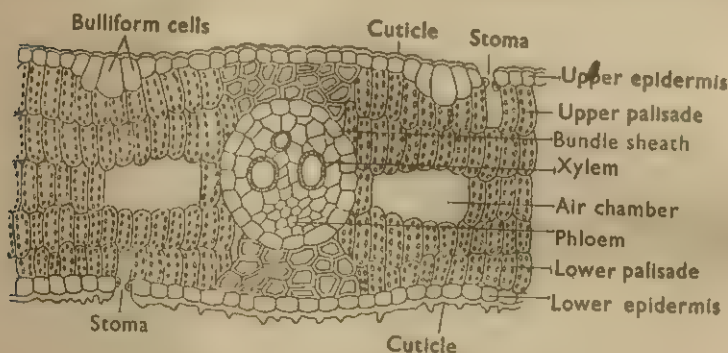


FIG. 261. T.S. OF BAMBOO LEAF (in part)

Upper epidermis. It consists of one layer of cells, some of them being bulliform in shape, and possesses a thick cuticle. Stomata are present here and there.

Mesophyll. This tissue cannot be differentiated into palisade and spongy parenchymas, but is composed of palisade parenchyma only. The cells are elongated, closely packed, and are at right angles to the upper and lower epidermal layers. The cells situated towards the upper epidermis are often designa-

ted as the *upper palisade* and those towards the lower one, the *lower palisade*. Many oval *air chambers* are found between the two palisade parenchymas.

Vascular bundles. These are of different sizes, occurring at intervals, and are provided with sclerenchymatous cells towards the upper and lower surfaces of the leaf. Each bundle is conjoint, collateral and closed. The xylem is situated towards the upper surface and the phloem towards the lower one.

5. LEAF OF DATE PALM

A transverse section through a leaf of date palm (*Phoenix sylvestris*) of Fam. Palmae shows the following structure (Fig. 262) when observed under the microscope :

Upper epidermis. It consists of a single layer of tabular cells with cuticularized outer walls. Stomata occur at intervals.

Sub-epidermal layer. This layer is also composed of a single layer of parenchymatous cells, containing scanty chloroplasts.

Mesophyll. This tissue lies between the two layers of sub-epidermal layers and makes up the main bulk of the leaf. It cannot be differentiated into palisade and spongy parenchymas. Patches of sclerenchyma are present more or less in parallel series towards both the upper and lower sub-epidermal layers.

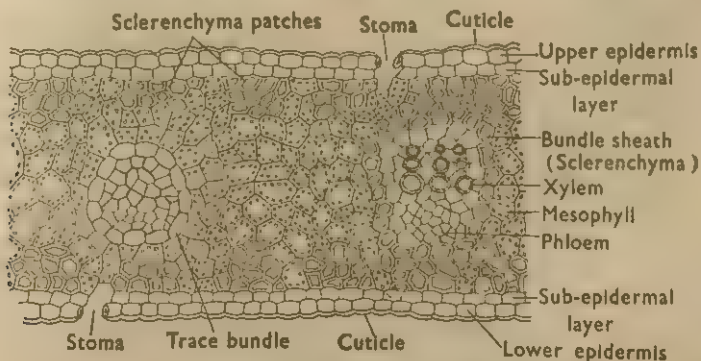


FIG. 262. T.S. OF DATE PALM LEAF (in part)

Vascular bundles. The vascular bundles are arranged in a parallel series. Each bundle is conjoint, collateral and closed, with the xylem facing the upper epidermis and the phloem, the

lower one. There are *two* kinds of vascular bundles—large and small; the former ones are enclosed by a sclerenchymatous sheath each, while the latter, by a parenchymatous one. The sclerenchyma is present on the upper and lower sides of each large bundle forming I-girders.

Sub-epidermal layer. It is similar to the upper sub-epidermal layer.

Lower epidermis. It is similar to the upper epidermis.

6. LEAF OF TYPHA

A transverse section of the leaf of *Typha* (Fam. Typhaceae), a marsh plant, shows the following structure (Fig. 263) when observed under the microscope :

Upper epidermis. It consists of a single layer of parenchyma cells joined end to end and with a thick layer of cuticle deve-

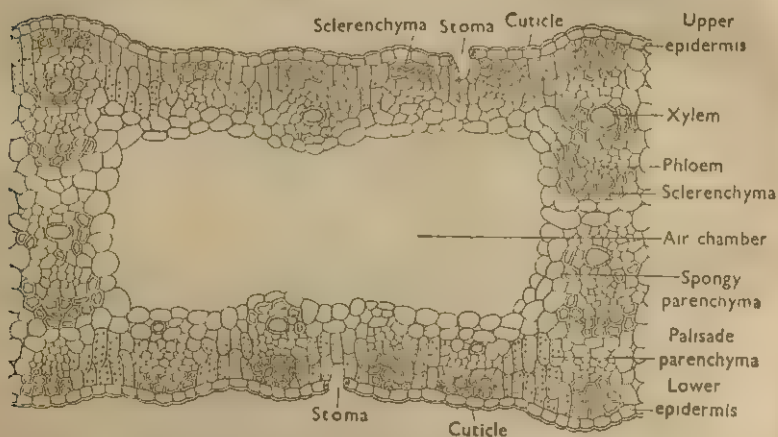


FIG. 263. T.S. OF *Typha* LEAF (in part)

loped on the outer face. The layer is not continuous but is interrupted at intervals by stomata.

Mesophyll. This tissue is differentiated into palisade and spongy parenchymas.

(a) *Palisade parenchyma* is composed of cells, which are prismatic in outline and contain an abundance of chloroplasts.

They occur in closely packed-up patches, both below the upper and lower epidermal layers.

(b) *Spongy parenchyma* is composed of oval to isodiametric cells with prominent intercellular spaces, but without any chloroplasts. They occur in association with the vascular bundles as well as lie enclosing a large, somewhat rectangular air chamber.

Vascular bundles. These occur in rows, either singly or in twos forming a parallel system of I-girders. The flanges of these girders are made up of groups of sclerenchyma cells, which are sub-epidermal in nature. Besides, sclerenchyma also occurs in patches as well as in the form of scattered fibres in association with vascular bundles. Each vascular bundle is conjoint, collateral and closed. Both the xylem and the phloem elements are rather feebly developed.

Lower epidermis. It is similar to the upper epidermis in structure.

IV. STRUCTURE OF PETIOLE

PETIOLE OF NYMPHAEA

A transverse section of the petiole of *Nymphaea* (Fam. Nymphaeaceae) shows the following arrangement of tissues (Fig. 264) from the periphery towards the centre when observed under the microscope :

Epidermis. It consists of a single layer of cells with a thin cuticle and uniseriate multicellular hairs.

Hypodermis. It is made up of several layers of collenchyma cells containing chloroplasts.

Ground tissue. It consists of a mass of thin-walled cells with numerous air spaces containing peculiar *stellate spines* (branched sclerenchymatous cells with very small spicules of oxalate). Latex sacs are present all over the ground tissue.

Vascular bundles. These are poorly developed and scattered in the ground tissue, as in the monocotyledonous stems. The

bundles are of *two* types ; *single* and *double*. The primary xylem breaks downs and gives rise to air spaces. True vessels

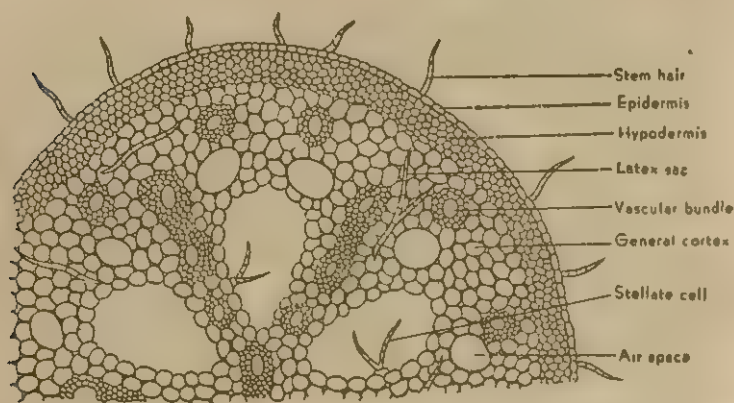


FIG. 264. T.S. *Nymphaea* PETIOLE (in part)

and cambium are absent. It should be noted that in mature specimens each bundle consists of a patch of phloem and a schizogenously developed canal.

H⁵ STELES AND THEIR EVOLUTION (Figs. 265 & 266)

The central core of the stem and the root containing the

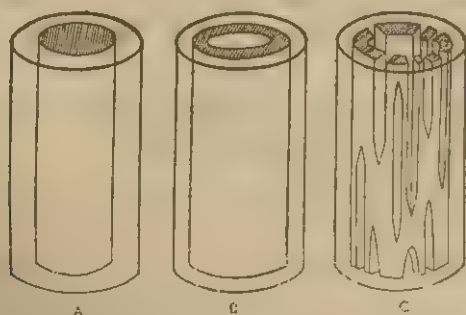


FIG. 265. TYPES OF STELE (Diagrammatic)
A, haplostele ; B, siphonosteles ; C, diactyosteles
(Redrawn from Eames and MacDaniels).

vascular tissues for support and conduction is known as the

stele or central cylinder. It is usually demarcated from the rest of the body by an endodermal layer. All the tissues lying outside the endodermis collectively constitute the **extrastelar region**, while those within it form the **intrastelar region**. There are constant and characteristic differences in the arrangements and positions of the vascular tissues in various organs of plants.

The vascular tissues in their simplest and most primitive conditions form a **protostele**, where a solid cylinder of xylem is surrounded by a solid cylinder of phloem, both being differentiated from a single procambium strand. In a transverse section, a protostele may appear as circular, angular, stellate or irregularly lobed or folded. It is chiefly found in the lower vascular cryptogams, in the sporelings of almost all existing ferns, and in the fossil forms. From a study of the fossil records and comparative embryology, it is concluded that all other types of steles were derived from it.

The simplest form of a protostele is known as a **haplostele**, e.g., *Lycopodium cernuum*, *Selaginella kraussiana*, and some species of *Lygodium* and *Hymenophyllum*. A protostele, where the xylem core is in the form of radiating ribs, is called an **actinostele** e.g., *Psilotum triquetrum*, *Lycopodium phlegmaria*, *Isoetes coromandeliana*, etc., while one, with the xylem divided into plate-like structures lying somewhat parallel to one another, is a **plectostele** e.g., *Lycopodium clavatum*, *L. volubile*, etc.

The next step in the evolutionary progress is the appearance of some unspecialized (parenchymatous) large cells at the centre of the xylem core ; this is the beginning of the development of pith, and such a stele with a pith in the centre is called a **siphonostele***. A siphonostele without any overlapping gaps is called a **solenostele**, which may be either **amphiphloic** (where the phloem occurs on both the inner and outer faces of the xylem, as in *Marsilea*, *Pilularia*, and older stems of *Marattia*, etc., or **ectophloic** (where the phloem occurs only on the outer face of the xylem, as in rhizomes of *Botrychium virginianum* and in the stems of spermatophytes in general). On the other hand, a siphonostele

*According to some authors, a siphonostele is also known as a **solenostele**

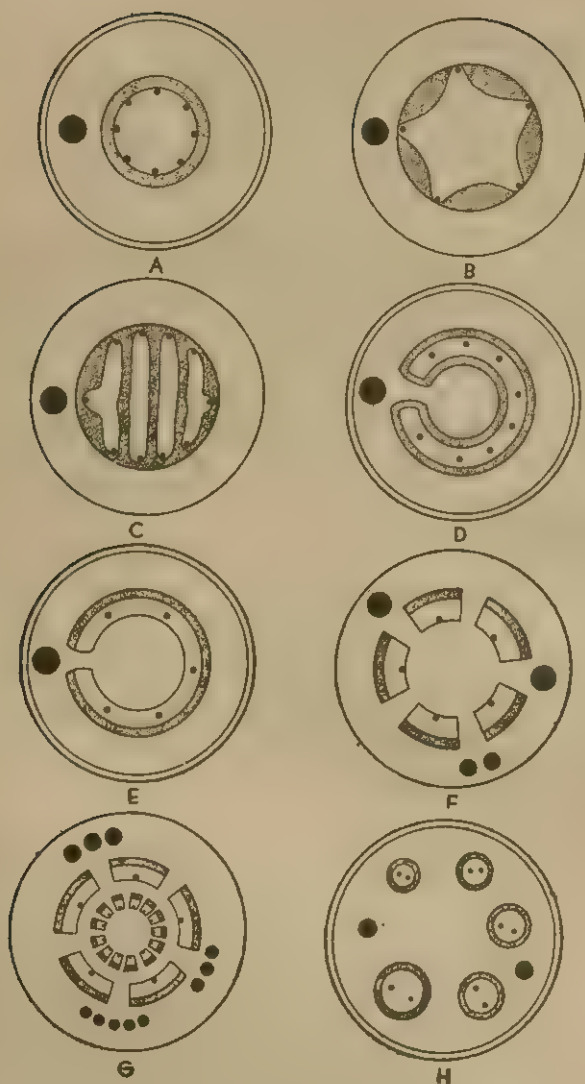


FIG. 266. DIFFERENT TYPES OF STELE (*Diagrammatic*)

A, haplostele; B, actinosteles; C, plectosteles; D, amphiphloic siphonosteles; E, plectophloic siphonosteles; F, dictyosteles; G, polycyclic dictyosteles; H, polysteles.

(*Modified after Smith*).

Shaded parts represent phloem; smaller dots indicate the positions of protoxylem; larger solid dots represent leaf traces.

with overlapping gaps is known as a **dictyostele***, e.g., *Ophioglossum*, older parts of *Osmunda claytoniana*, and some herbaceous angiosperms, etc.; the intervening strips of vascular elements, lying lateral to two overlapping gaps, are called **meristele**. When a series of dictyosteles occur in the form of concentric rings, a **polycyclic dictyostele** is formed, whose innermost cylinder may be a solenostele (e.g., *Matonia pectinata*) or a dictyostele (e.g., *Pteridium latiusculum*).

The next step in the scale of evolution is the development of the **polystele**, where several hadrocentric bundles are formed, each surrounded independently by an endodermis, e.g., *Polypodium vulgare*. This is probably derived from the siphonostele. Eames believes that the term *polystele* is rather a misnomer, and contends that no living plant has got a true polystele. According to him, a polystele is nothing but a dissected siphonostele.

There are two theories regarding the development of the siphonostele from the protostele. According to the **expansion theory**, the pith represents the unspecialized xylem, and as such, strictly stelar, as in *Gleichenia*. On the other hand, according to the **invasion theory**, the pith is extrastelar in origin representing the cortical tissue, which has invaded the stelar region during the course of development, particularly through leaf- and branch-gaps. The latter theory has been definitely proved to hold good in case of seed plants and in the majority of the pteridophytes.

* A dictyostele is also regarded as a much-dissected siphonostele. It is considered that in the stems of monocotyledonous plants, generally the vascular bundles of the dictyostele are scattered, resulting in a total loss of any semblance to a normal stele. The dissection may be brought about either by overlapping of leaf- and branch-gaps, or by dropping out of some segments of the cylinder.

CHAPTER VI

SECONDARY GROWTH IN THICKNESS

In the majority of dicotyledons, gymnosperms, and a few monocotyledons (e.g., *Dracaena*, *Yucca*, etc.), after the completion of primary growth of the axis in length and to some extent in thickness, subsequent growth in diameter is brought about by the formation of the secondary tissues. These secondary tissues are formed due to the activity of different cambium layers, both

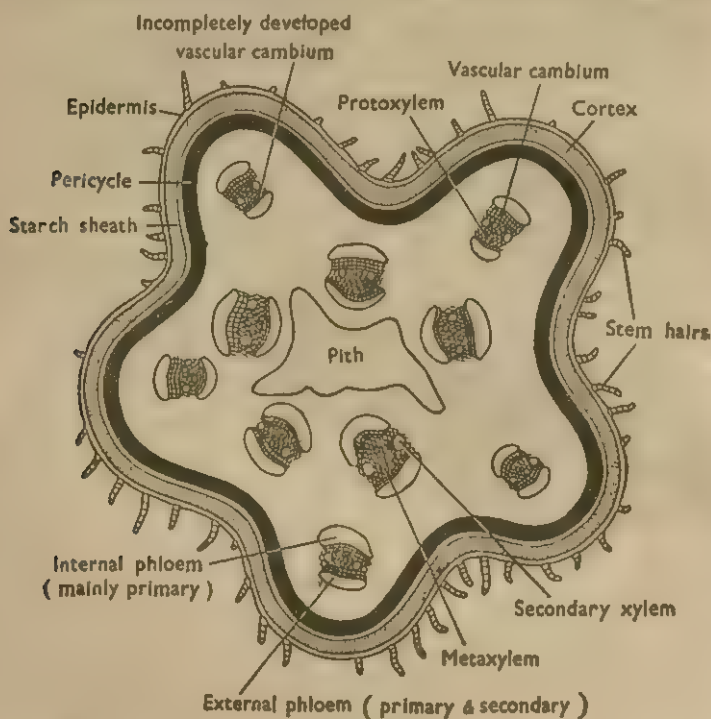


FIG. 267. T.S. OF A *Cucurbita* STEM AFTER SECONDARY GROWTH (Diagrammatic).

in the intrastelar and extrastelar regions, and the members in which these tissues occur increase in thickness. This increase in thickness, due to the formation of new secondary tissues by the activity of different cambium layers, is known as the secondary

growth. These secondary tissues are of *two* types, viz., secondary vascular tissues and periderm.

Three general types of secondary growth are recognized : (1) The primary vascular tissues form an almost continuous ring with very narrow medullary rays, and the secondary vascular tissues also form continuous rings, as in *Tiliaceae*

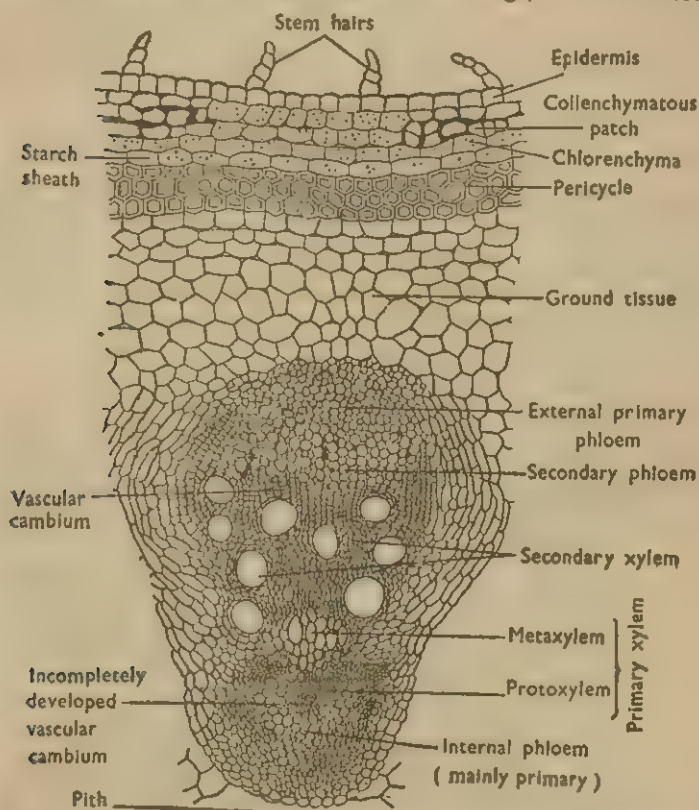


FIG. 268. T.S. OF A *Cucurbita* STEM AFTER SECONDARY GROWTH (*in part*)

and many woody dicotyledons. (2) The primary vascular tissues form a ring of distinct vascular bundles with wide medullary rays, but the secondary vascular tissues form a continuous ring with very narrow medullary rays, as in many herbaceous dicotyledons, conifers, *etc.* (3) The primary vascular tissues form a ring of distinct bundles, the interfascicular cambium (during

secondary growth) only forms ray parenchyma, and the fascicular cambium gives rise to vascular tissues ; so, the secondary vascular tissues are also divided into separate stands, as in *Vitis*, *Aristolochia* (vine type of stems), *Cucurbita*, etc. In *Cucurbita*, the little secondary growth is restricted generally to the vascular bundles, and the sclerenchymatous pericycle is not ruptured or disturbed (Figs. 267 & 268).

SECONDARY GROWTH IN DICOTYLEDONOUS STEMS (Figs. 269—276)

A. IN THE INTRASTELAR REGION

FORMATION OF CAMBIUM RING. When the secondary growth is about to begin, a few parenchyma cells of the primary medullary rays between the fascicular cambium layers of the vascular bundles become meristematic and form new strips of secondary meristems, known as the **interfascicular cambium**. These strips of interfascicular cambium join up the fascicular cambium layers of the primary vascular bundles on both sides, and thus, a complete **ring of cambium** is formed inside the central cylinder.

FORMATION OF SECONDARY XYLEM AND SECONDARY PHLOEM (Fig. 269). The cambium ring cuts off cells both inside

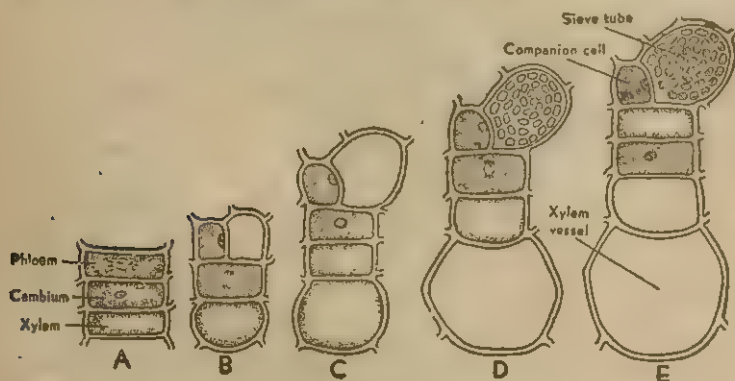


FIG. 269. STAGES IN THE FORMATION OF SECONDARY XYLEM AND SECONDARY PHLOEM

(Redrawn from Holman and Robbins).

and outside. Each cambium cell divides tangentially into an inner

cell and an outer one. Of these cells, one remains as the cambium mother-cell, and the other grows and differentiates into **secondary xylem** or **phloem** element. The xylem increases in bulk by the addition to its outer surface, and the phloem does so by the addition to its inner surface. The central cambium remains meristematic as long as the growth continues. The production of xylem is far more greater than that of phloem. The secondary xylem elements are vessels, wood fibres, tracheids and wood parenchyma. The secondary phloem elements are mainly sieve tubes, companion cells, bast fibres and phloem parenchyma. Sometimes, secretory cells, laticiferous ducts or resin canals are also present.

FORMATION OF ANNUAL RINGS (Fig. 270). In spring, when the buds unfold, many young green leaves are produced. As the work of assimilation begins vigorously, the need for abundant supply of raw food materials dissolved in water causes the cambium to form xylem vessels with wide cavities, and thus we find big vessels in spring. But during summer, and specially towards the end of the growing season, the activity of the cam-

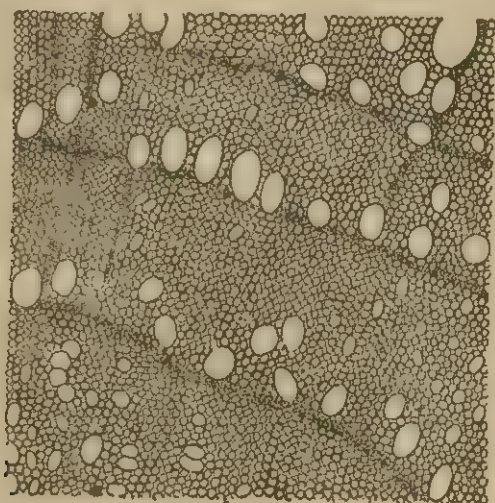


FIG. 270. ANNUAL RINGS

bium gradually declines and sufficient mechanical tissues, mainly the fibres, are formed. The former kind of wood is called the **spring wood** and the latter, the **summer wood**, and they differ more

or less from each other in cell-size, cell-type, and cell-arrangement. With the approach of winter, the activity of the cambium ceases, and it passes into a resting condition. On the return of the next spring, this process is repeated, and thus, we get alternate layers of xylem vessels with wide cavities and mainly wood fibres in spring wood and summer wood respectively. The spring wood and the summer wood together constitute the growth of wood in one year. Thus, in a cross section of the stem of a tree one finds so many concentric rings. These rings are called **annual rings** or **growth rings**. Such annual rings are formed year after year, and by counting their numbers, the age of a tree can approximately be determined. It should be borne in mind that annual rings are not found in all woody plants. Those plants, which live in places where seasonal changes are not well marked, have no annual rings.* In the secondary phloem, there is usually no difference between the spring phloem and the summer phloem, hence it forms a uniform continuous band.

When the vessels are distributed more or less uniformly throughout an annual ring, the wood is said to be of the **diffuse porous** type (Fig. 271, A). In some cases, however, the gradual change in size from the early to the late wood is noted. On the other hand, a wood is said to be of the **ring-porous** type (Fig. 271, B), when there is a distinct differentiation in the sizes of the vessels of the early and late woods in the ring; those of the former are definitely large than those of the latter.

There are *two* theories about the formation of annual rings :

(a) **Food theory.** The vessels, which are formed in spring, have larger diameters than those formed in summer, because more food-supply is available in the soil during the spring than during

*Dr. K. A. Choudhury, while working with "The formation of growth rings in Indian trees", has indicated that "deciduous trees do not always show growth rings, nor are all evergreens without them. . . . An analysis of external factors, such as temperature, rainfall and humidity, has not brought out any direct correlation with the commencement and cessation of growth". Some of his observations are indicated below :

In *Pinus longifolia* (pine), growth rings are distinct, and these indicate the true age of a tree. In *Tectona grandis* (teak), *Acacia catechu* (cutch), *Bombax malabaricum* (silk cotton), *Dalbergia sisoo* (sisoo), *Albizia lebbek* (sirish), fairly distinct growth rings are present. The ring-like marks in *Eugenia jambolana* (jaman), *Shorea robusta* (sal), are not annual, and these do not indicate the age of a tree. In *Michelia champaca* (champa) distinct growth rings are present, and each year's growth is terminated by a concentric band of parenchyma cells.

the summer, and the continual conduction of water under high pressure demands for wider vessels. The walls of the

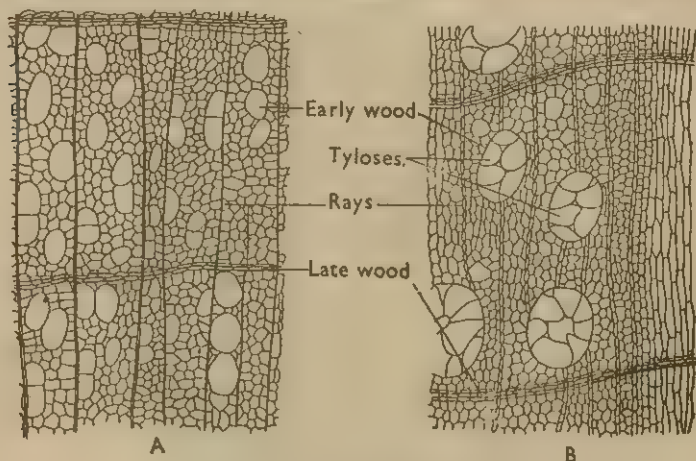


FIG. 271. DIFFERENT TYPES OF WOOD

A, diffuse porous ; B, ring-porous.

vessels are elastic, but under high pressure they lose their elasticity and remain wider.

(b) **Space theory.** Owing to the continual addition of new wood, the space within the plant becomes gradually lesser and lesser (consequently, the pressure becomes higher and higher), and thus, the vessels formed in the later season have their dimensions gradually smaller and smaller ; so, the vessels formed in summer have the smallest dimensions. But, when during winter the cork and bark crack, the space inside the plant becomes wider (pressure becomes relaxed), and hence, the vessels formed in the following spring have larger diameters.

As the annual rings are formed, the older ones are pushed towards the centre. The cells of the older layers gradually lose the power of conduction of water, and ultimately become hard and appear as dark mass in the centre owing to the deposition of tannin and other substances. The central portion is called the **duramen** or **heartwood**. The outer portion, consisting of younger xylem rings, conducts the sap and appears as a light-coloured mass. This outer portion is known as the **alburnum** or **sapwood** (Fig. 272).

FORMATION OF SECONDARY MEDULLARY RAYS. The interfascicular cambium produces secondary xylem and phloem,



FIG. 272. ANNUAL RINGS IN A T.S. OF ABOUT 50-YEAR-OLD STEM OF *Pinus excelsa*.
(Specimen received through the courtesy of Indian Forest Research Institute, Dehra Dun).

and the wide primary medullary rays are no longer found to run between the pith and the cortex, but certain cambium cells, instead of giving rise to secondary xylem and phloem elements, produce rows of parenchyma cells, which form very narrow **secondary medullary rays**. Through these the phloem and other tissues are supplied with water absorbed from the wood.

B. IN THE EXTRASTELAR REGION

FORMATION OF PERIDERM. (Fig. 273). When secondary growth takes place, the secondary xylem and phloem tissues are formed due to the activity of the cambium layer, and the formation of these new tissues inside set up an internal pressure, which causes the epidermis to rupture. To provide for this, new secondary tissues are developed (usually in the cortical region), which are collectively termed as the **periderm**. The formative

layer of periderm is the **phellogen** or **cork cambium**, as its cells, by repeated divisions, do not form wood or bast, but give rise to the cork. This phellogen, which is a secondary meristem, generally arises in the layer of cells just underneath the epidermis. It may arise in other tissues also. Thus, in willows, the phellogen arises in the epidermis itself. In *Clematis*, vine, etc., the phellogen

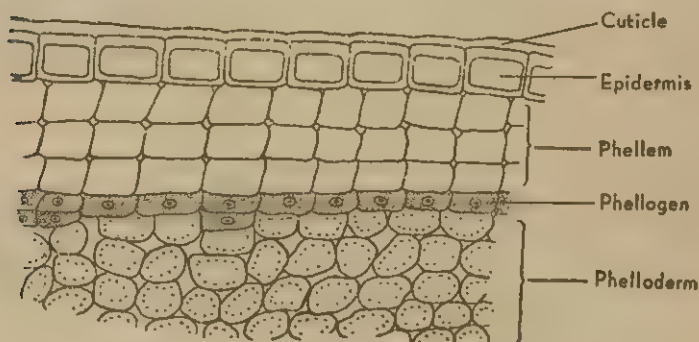


FIG. 273. FORMATION OF PERIDERM
(Redrawn from Holman and Robbins).

layer arises first in the pericycle, and in potato tuber, it arises both in the epidermis and in the sub-epidermal layer. On its outer side the phellogen gives rise to new cells, which lose their contents, become filled with air and are arranged in rows at right angles to the surface forming a dead, imprevius layer, well adapted as a protective coat. Their walls become mainly suberized and this dead tissue, which lacks inter-cellular spaces, is known as the **phellem** or **cork**. This phellem and phellogen together comprise the secondary epidermal tissues. The phellogen also produces loosely arranged premanent, parenchyma cells containing chloroplasts, and these are added to the primary cortex. This is a secondary ground tissue, and is known as the **phelloderm** or **secondary cortex**. The phellogen, phelloderm and phellem together constitute the **periderm**.

FORMATION OF BARK. After the formation of the periderm, all the tissues lying outside it can receive no supply of water, hence, they eventually dry up and die. With the advancement of age, followed by an increase in diameter of the stem, succes-

sive periderm layers are formed deeper within its body. Consequently, a few overlapping and alternate layers of periderm and dead cortical or phloem tissues are formed ; All these tissues are collectively referred to as the **rhytidome**, forming a thick outer crust on the stem, which is loosely and popularly known as the **bark**. As the bark produced is usually thrown in scales, it is called the **scale bark** or **shell bark**, as in the guava, *Eucalyptus*, pine, etc. Thus, in perennial plants, the boughs are covered at first with epidermis, in the first year with periderm, and when several years old, the older branches and the main trunk are covered with bark.

Functions of cork and bark. (a) Bark has a protective role of great importance because of the slowness of exfoliation. (b) Partly because of the absence of the air spaces but more because of suberization, cork is the most impermeable of all the tissues, and thus, it is of great value in checking transpiration. (c) Cork is also a poor conductor of heat. (d) It prevents the invasion of living tissues by parasitic fungi and bacteria. (e) Bark also helps in the removal of waste products during exfoliation.

LENTICELS. (Figs. 275 & 276). As the epidermis is replaced by the periderm, so there must be some mechanism to replace the stomata for performing their functions, *i.e.*, to maintain the interchange of gases and the liberation of water vapour. Thus, in the periderm, to provide for these, just beneath where stomata existed, cork does not develop for a time ; the phellogen gives rise instead to a loose tissue, composed of thin-walled, round, unsuberized and air-filled cells, the **complementary cells**, between which are conspicuous air spaces. This tissue, by reason of the cell-turgidity and presence of air spaces, takes up much more space than does the cork, rarely having adequate room for full development beneath the epidermis. Consequently, the epidermis is soon ruptured, and the complementary tissue protrudes forming with the upturned, ruptured edges of the epidermis a characteristic lens-shaped scar, visible to the naked eye. The entire structure, of which the loose complementary tissue forms the most significant part, is known as the **lenticel**. The loose cells of the complementary tissue are held in place by the formation of diaphragms

of denser tissue by the phellogen and are known as the **closing layers**. Lenticels form small oval scars on the surface of trees.

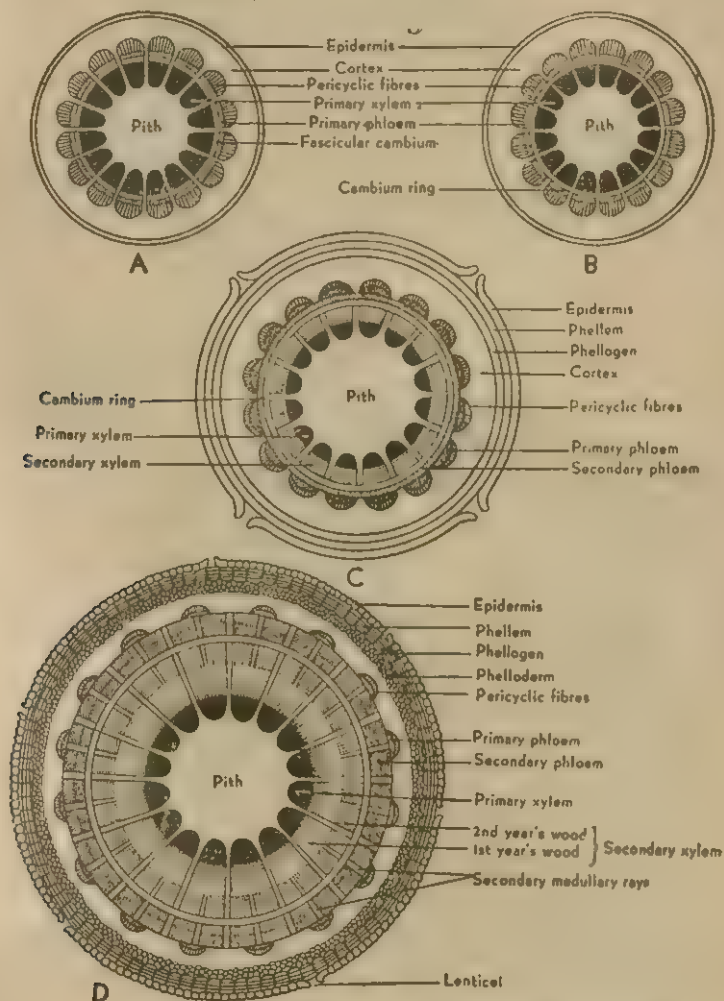


FIG. 274. STAGES OF SECONDARY GROWTH IN A DICOTYLEDONOUS STEM
(Diagrammatic)
(Redrawn from Holman and Robbins).

They are also found in many roots and on fruits. The dots which are found on apples and plums are nothing but lenticels.

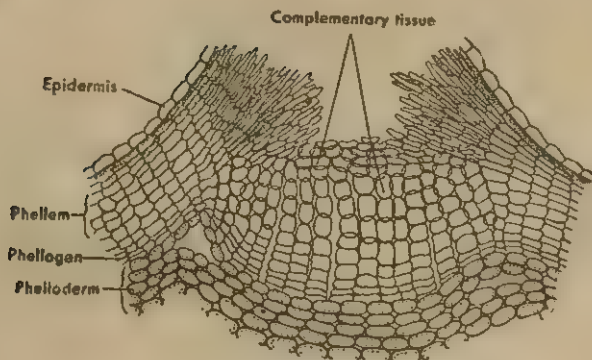


FIG. 275. LENTICEL
(Redrawn from Holman and Robbins).

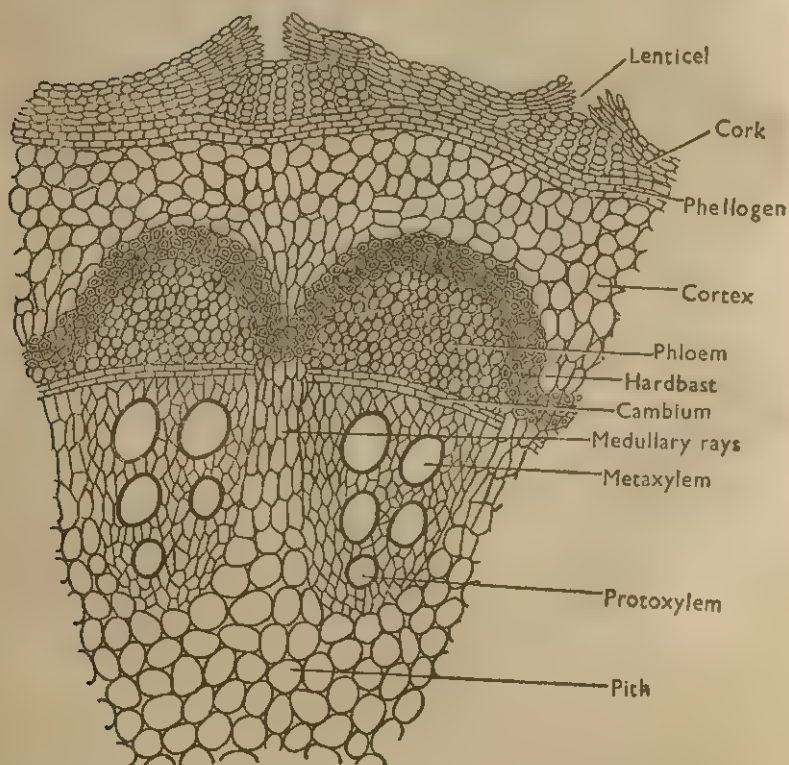


FIG. 276. LENTICELS AS SEEN IN A T.S. OF A *Tinospora* STEM
(in part).

Though they remain open for some years, in many cases, they are closed due to the formation of a cork layer. In many cases, they persist for several years.

ANOMALOUS SECONDARY GROWTH

Some dicotyledons and gymnosperms show a type of secondary growth that deviates considerably from the normal type just considered. This is called the **anomalous secondary growth**. This is common in climbing plants and lianes, combining strength with pliability, and in storage organs (beet, sweet potato, etc.).

Firstly, the cambium is normal to begin with, but, it is unequally active at different parts giving different proportions of secondary xylem and secondary phloem with an unusual arrangement.

(a) When the cambium in some parts produces a larger amount of xylem than phloem, and at other parts a larger amount

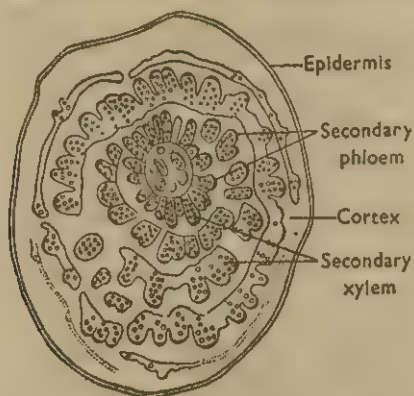


FIG. 277. T.S. OF *Bauhinia* STEM (Diagrammatic)

of phloem than xylem, a more or less lobed or divided xylem cylinder alternating with bands of phloem results, as in some Bignoniaceae. When the cambium has little activity at some parts, or the original continuous xylem ring is split into irregular parts due to growth (proliferations) of xylem parenchyma, a similar structure is obtained, as in *Bauhinia* (Fig. 277), of S. F. Caesalpinieae (Fam. Leguminosae), and many members of the Fam. Bignoniaceae.

(b) Due to unusual activity of cambium strands, the secondary phloem may be embedded or included in the secondary xylem (interxylary or included phloem), as in *Combretum*, *Entada*,

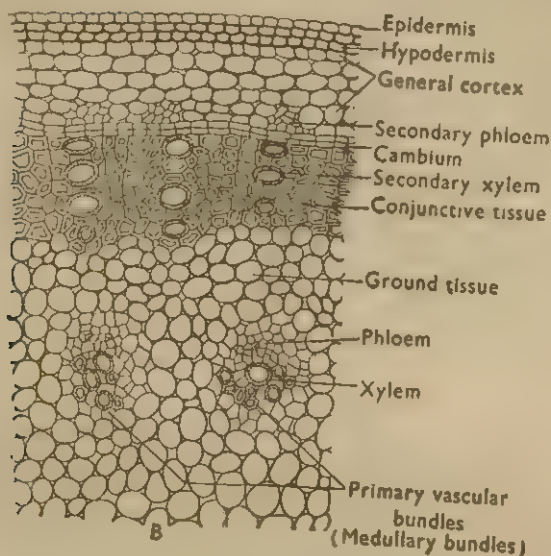
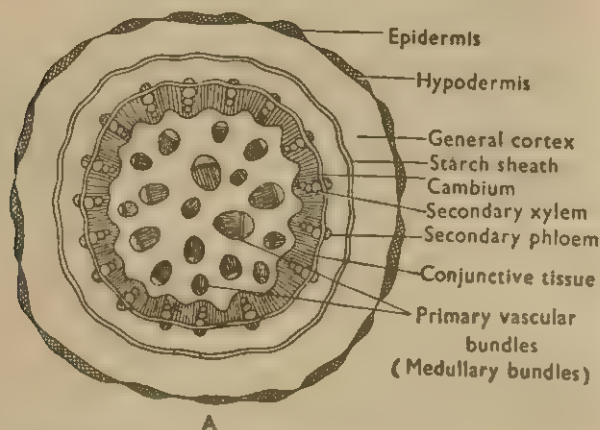


FIG. 278. T.S. OF *Mirabilis* STEM

A, an entire section (diagrammatic); B, a portion of the same (magnified).

Strychnos, etc. Portions of cambium may produce phloem towards the inside for a short period instead of xylem, but soon

returns to normal activity, so that, some secondary phloem becomes included in the secondary xylem.

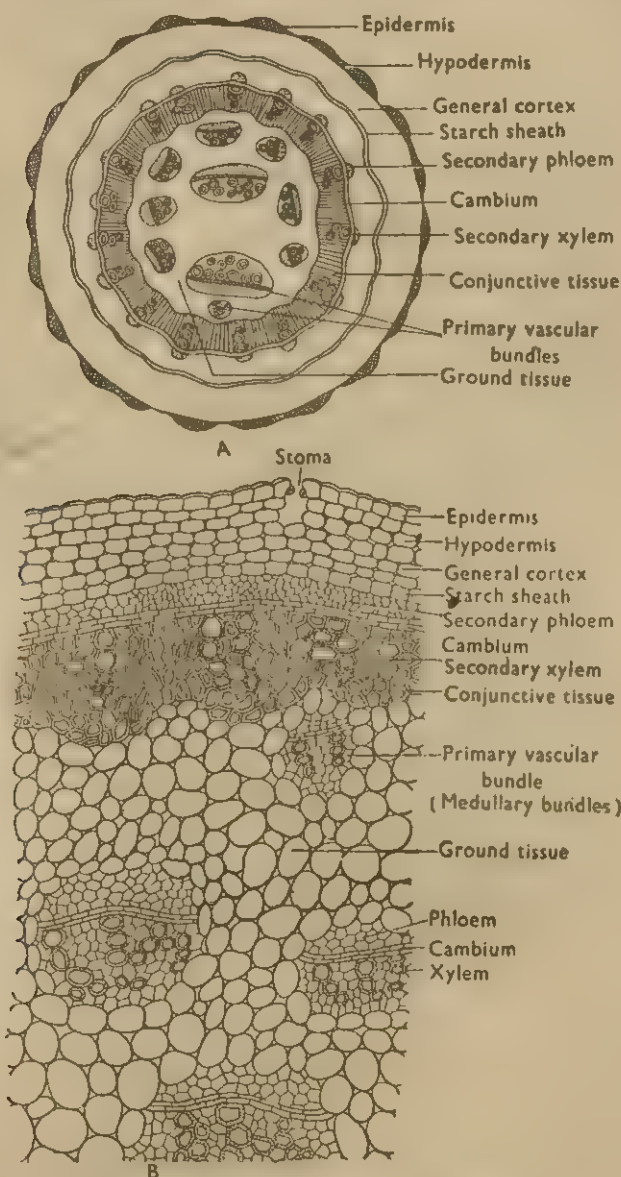


FIG. 279. T.S. OF *Boerhaavia* STEM

A, an entire section (diagrammatic); B, a portion of the same (magnified).

Secondly, strips of cambium develop in abnormal positions, or the original cambium layer is replaced by cambium layers successively formed in the periphery.

(a) The original cambium is in the form of small strips enclosing some primary tissue. These strips function normally

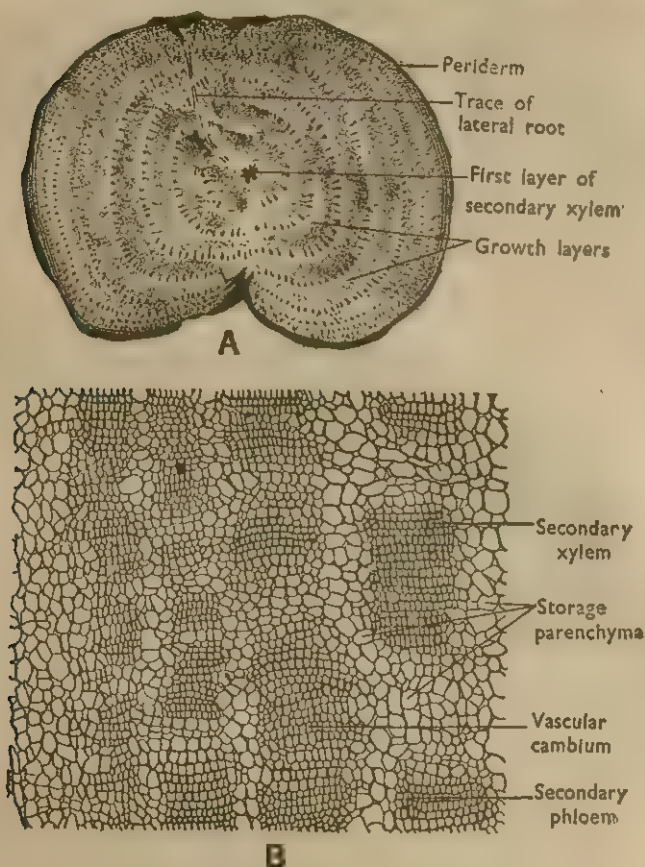


FIG. 280. T.S. OF SUGAR-BEET ROOT

A, diagrammatic representation of an entire section ; B, magnified view of a peripheral portion of A.

and independently producing secondary xylem and phloem as usual in rings. So, finally the stem appears to be composed of several stems fused together, e.g., *Serjania* (Fam. Sapindaceae).

(b) The original cambium is in the form of a ring in normal position, producing secondary xylem and secondary phloem as usual, but, it is also soon replaced by another cambium layer outside with normal activity. This may be repeated. Thus, alternate concentric rings of xylem and phloem, either continuous or as separate bundles, are formed, as in *Chenopodiaceae*, *Amaranthaceae*, *Sapindaceae*, *Nyctaginaceae* (Figs. 278 & 279), *Menispermaceae*, *Gnetum* (a gymnosperm), and the majority of lianes.

Anomalous structures may be due to medullary or cortical bundles, as in *Piperaceae*, *Ranunculaceae*, *Nyctaginaceae*, *Amaranthaceae*, etc.

In sugar-beet root (Fig. 280), at first cambium forms a ring of bundles near the primary xylem. Later, a series of cambia arise successively outside producing parenchyma and vascular bundles, with a predominance of parenchyma in both the xylem as well as the phloem. All these cambial layers remain simultaneously active for a long time.

SECONDARY GROWTH IN MONOCOTYLEDONOUS STEMS

The secondary growth in monocotyledonous stems is of rare occurrence. But, it is well exemplified by *Dracaena* (Fig. 281), *Yucca*, and a few other monocotyledonous plants. In case of *Dracaena*, the cambium (a secondary meristem) originates in the ground tissue, ten to fifteen cells deep below the epidermis. This cambium layer gives rise to parenchyma cells on its outside, and secondary vascular bundles and conjunctive tissue towards the inside. When fully differentiated, these secondary vascular bundles are leptocentric.

In palm stems (Fig. 282), firstly, thickening takes place by means of a peripheral primary thickening meristem lying below the leaf primordia of the apical meristem. This apical meristem, by tangential divisions, forms a tissue consisting of ground parenchyma and procambial strands that mature into vascular bundles.

This primary thickening is followed by an elongation of the axis, and a limited increase in thickness by enlargement and division of the ground parenchyma cells. In some cases, the sclerenchyma associated with the bundles may enlarge its area by a

widening of the cell cavities, thickening of the cell walls, or addition of new strands. The simple type of thickness, which

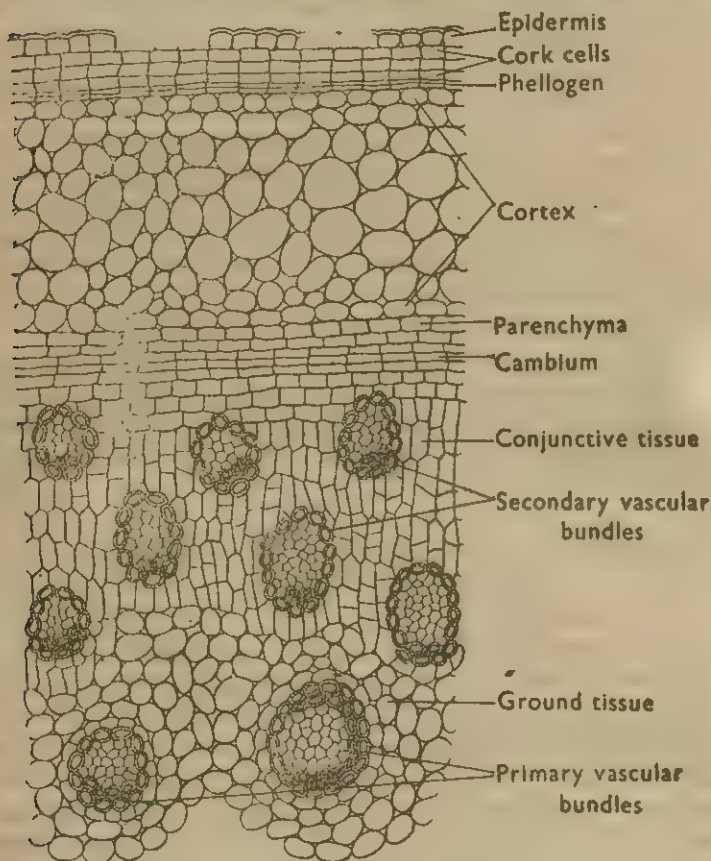


FIG. 281. SECONDARY GROWTH IN *Dracaena* STEM

is in reality the long-continued primary growth, adds considerably to the inflexibility of the tall trunk with its crown of foliage.

SECONDARY GROWTH IN DICOTYLEDONOUS ROOT (Figs. 283—286).

When the secondary growth in a root is about to begin, certain cells in the conjunctive tissue, just inside the phloem groups,

become meristematic and form four bands of actively dividing cambium, immediately internal to each phloem group. This

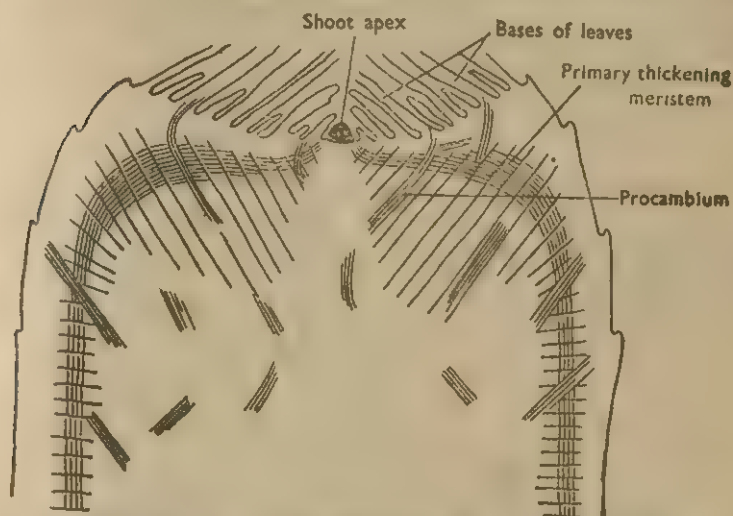


FIG. 282. DIAGRAMMATIC REPRESENTATION OF THE APICAL PORTION OF A PALM SHOOT SHOWING THE DIFFERENT MERISTEMS (From Esau).

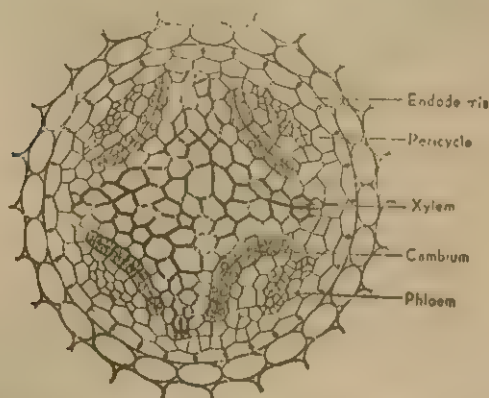


FIG. 283. COMMENCEMENT OF SECONDARY GROWTH IN DICOTYLEDONOUS ROOT (Diagrammatic) (Redrawn from Holman and Robbins).

cambium extends both ways, and meets the pericycle next to the protoxylem. A change also takes place here. The pericycle,

at first one cell thick, now divides and becomes two or more cells thick at this point. The cells of the innermost layer now undergo regular divisions, and form a continuous wavy band of cambium in the root, running internal to phloem and external to xylem. This cambium goes on dividing and producing secondary xylem internally and secondary phloem externally, just as it does in the

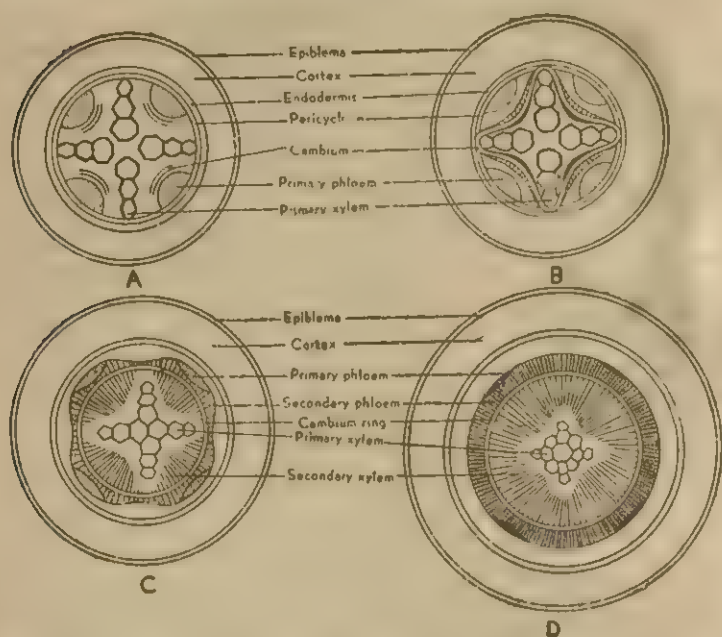


FIG. 284. STAGES OF SECONDARY GROWTH IN DICOTYLEDONOUS ROOT (Diagrammatic)

(Modified after Holman and Robbins).

case of the stem.* The division begins in the depression just opposite the phloem group and is very active there, so that, the strip of cambium, which was wavy at the onset, now becomes a circular ring, just as one finds in the stem. Normally, there are no primary medullary rays. But, when the secondary cambium divides and produces internal xylem and external

But in roots, the secondary xylem is larger, contains more numerous vessels, few fibres, more parenchyma, and more abundant rays, while the secondary phloem contains less fibres and more parenchyma.

phloem, some of the cambial cells, just next to the protoxylem groups, instead of giving rise to secondary xylem and phloem, usually produce strands of parenchyma cells, called the **main medullary rays**. They radiate outwards through the secondary wood. Sometimes, small secondary medullary rays are also formed from the cambium ring. The primary phloem bundles can be recognized as patches between two main medullary rays. Another point deserves notice. The primary xylem develops from without inwards (*centripetal*), and the secondary one from within outwards (*centrifugal*). Thus, one finds a centripetal primary and a centrifugal secondary wood, as in the case of stems.

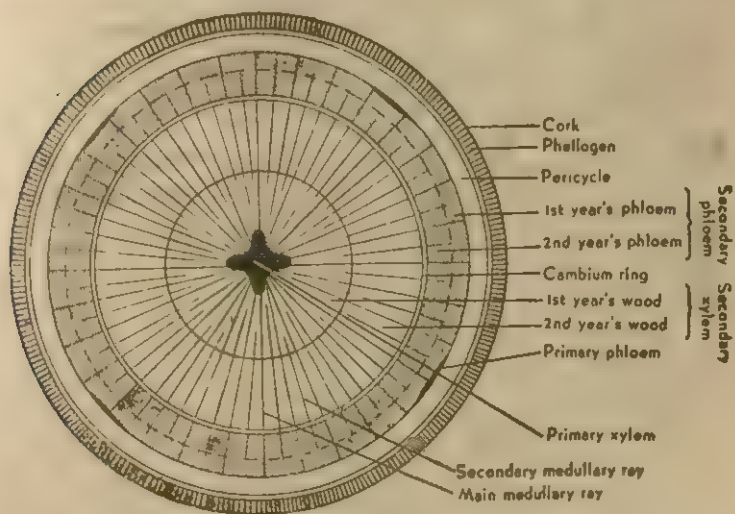


FIG. 285. FINAL STAGE OF SECONDARY GROWTH IN DICOTYLEDONOUS ROOT
(Diagrammatic)

(Modified after Holman and Robbins).

The older parts of the root gradually acquire a protective covering of periderm in the usual way, but the phellogen layer in the root usually originates in the pericycle*, which is an exception in the case of stems. The first bark is comparatively thick, as the

Sometimes, the periderm layers arise in the phloem tissue, so that the pericycle also takes part in the formation of bark,

cortex with the endodermis dies, and peels off early. But the subsequent barks become thinner gradually.

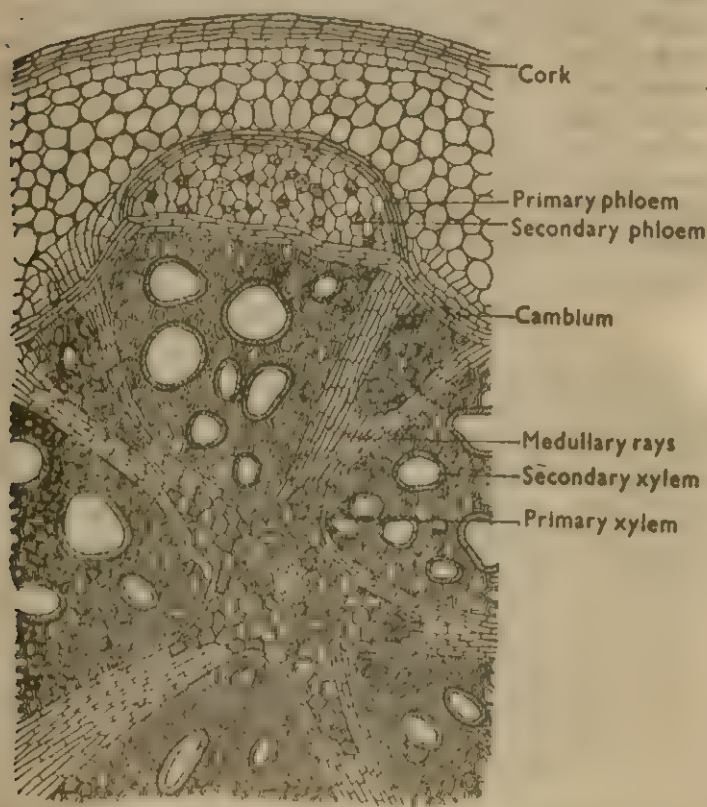


FIG. 286. T.S. OF *Tinospora* ROOT SHOWING SECONDARY GROWTH (in part)

CHAPTER VII

HEALING OF WOUNDS, TYLOSES, AND LEAF-FALL

HEALING OF WOUNDS (Fig. 287).

When a member or part of a plant is injured, it heals up its wound in the following ways :

(a) In lower plants, such as thallophytes, when a part is severed from the mother plant, the lost part is soon regenerated.

(b) In higher plants, the wounded cells die and become brown and dry, and the underlying cells become lignified, which protect the inner part from desiccation.

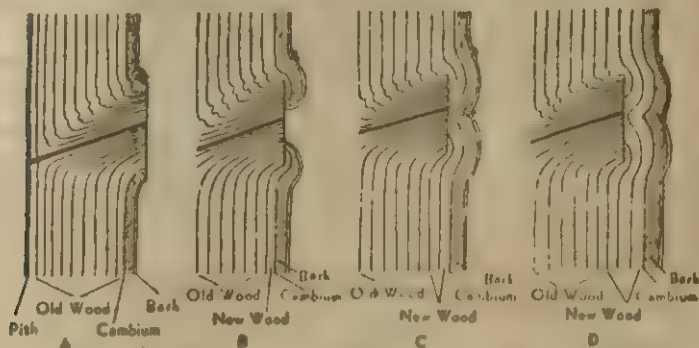


FIG. 287. STAGES IN THE HEALING OF WOUNDS
(Diagrammatic)

(Redrawn from Smith, Gilbert, et al)

(c) The simple wounds of plants containing laticiferous tissues are healed up by the coagulation of latex at the wounded point.

(d) When a stem is injured, the outermost uninjured living cortical cells form a meristematic layer, the phellogen, which produces a layer of cork outside and protects the inner uninjured part.

(e) In woody plants, when the wounds are deep, the living cells lying just beneath the injured ones become meristematic and produce a mass of parenchyma, known as the **callus**, which fills

up the wound. Subsequently, a layer of cork is developed on the outside, and thus the wound is healed up. But, if the wound be very deep so as to injure the cambium, then a new cambium is formed in the cells of the callus, and is thus joined up with the uninjured cambium.

When a branch of a tree is cut or broken off, the callus is produced from the cambium layer round the margin of the exposed surface. In this case, the cambium gives rise to a secondary tissue, which afterwards completely buries the stump. This is the origin of **knots**, so frequently met with in the wood of trees. The hardness of the knot is due to the pressure of the surrounding wood.

If the wounds are not closed, the injured cells are liable to be infected by bacteria or attacked by fungi, *etc.*, which will cause decay and destruction of the plant. For this reason, the gardeners usually cover the wounds before callus-formation by cement, coal tar, paraffin wax, *etc.*, in order to prevent the attack of bacteria or fungi.



TYLOSES (Fig. 288).

When the alburnum or sap wood changes into duramen or heart wood, the living cells adjoining tracheal elements grow and penetrate the cavities of the latter and multiply there. Such balloon-like outgrowths more or less completely close the cavities of the vessels and form what are known as **tyloses** or **tracheal plugs**. These structures are formed by the enlargement of the pit membranes of the half-bordered pits between wood parenchyma or medullary ray cells. They commonly occur in the wood of angiosperms. Their formation may be induced in many plants by wounding. Their development is said to be due to a difference in pressure in the cells on either side of a pit membrane. They are of considerable econo-

FIG. 288. TYLOSES
A, in l.s.; B, in t.s.
(Modified after
Holman & Robbins).

mic importance, since, by blocking the vessel lumens, they prevent rapid entrance of water, air and fungal parasites.

LEAF-FALL

In our country (generally in winter) as well as in others, when the period of leaf-fall advents, some unseen stimulus, caused by the scanty absorption of water which necessitates the reduction of the transpiring surface, causes the formation of a

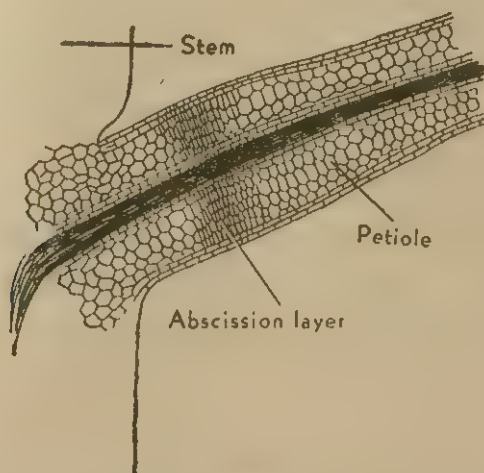


FIG. 289. FORMATION OF ABSCISSION LAYER DURING LEAF-FALL
(Modified after Holman and Robbins).

phellogen layer right across the base of the petiole. The phellogen layer gives rise to a layer of cork continuous with the cork of the stem. Cork being impervious to water cuts off the supply of nutrient solution to the leaf, and the layer of parenchyma cells just outside is disorganized; this disorganized layer is known as the **abscission layer** (Fig. 289). The leaf is now held in position only by the vascular tissue, which enters in it from the stem. Then the vascular tissue breaks at the abscission layer under the weight of the lamina, or by being disturbed by the wind, and thus the leaf falls down. The scar left on the stem simply dries up, or

cork is formed by the underlying meristematic tissue to cover the exposed surface. The vessels in the scar are closed up with gum and mucilage. That the leaf-fall is a vital process is proved by the fact that the leaves of a dead branch do not fall. It is to be noted that before the leaf is shed, the waste products are transferred to the leaves, and when the leaf-fall takes place, they are got rid of.

CHAPTER VIII

ANATOMY IN RELATION TO PHYSIOLOGY

So long we have been considering the different organs in plants from purely the anatomical standpoint. They can, however, be examined from other angles, namely, physiological, ecological, medicinal, economical, *etc.* From the functional viewpoint, Prof. G. Haberlandt published a monographic work, entitled '*Physiologische Pflanzenanatomie*' in 1884. In this book, he considered the functions of the various plant organs under a few systems as follows :—

(i) the dermal system, (ii) the mechanical system, (iii) the absorbing system, (iv) the photosynthetic system, (v) the vascular or conducting system, (vi) the storage system, (vii) the aerating or ventilating system, (viii) the secretory and excretory systems, (ix) the stimulus-transmitting system, (x) the motor system, and (xi) the sensory system.

Of these, only the dermal, the mechanical, the photosynthetic, and the ventilating systems are considered here.

I. THE DERMAL SYSTEM

Every plant cell, even the minutest unicellular one, possesses a distinct limiting membrane, the **cell wall**, which protects it from the surrounding medium. In case of higher plants, there is a well-marked **dermal** or **tegumentary system**, which serves the function of affording protection to the vitally important internal organs. The epidermis along with its openings and outgrowths, the periderm, and the exodermis constitute the dermal system.

A. THE EPIDERMIS

As already stated before, the **epidermis** is made up of cells, usually tubular (in stems and roots) and lenticular (in leaves) in shape. The cells are mainly parenchyma containing inconspicuous protoplasmic matter and without any intercellular space,

On the outer surface of the epidermal layer, a layer of cutin (the

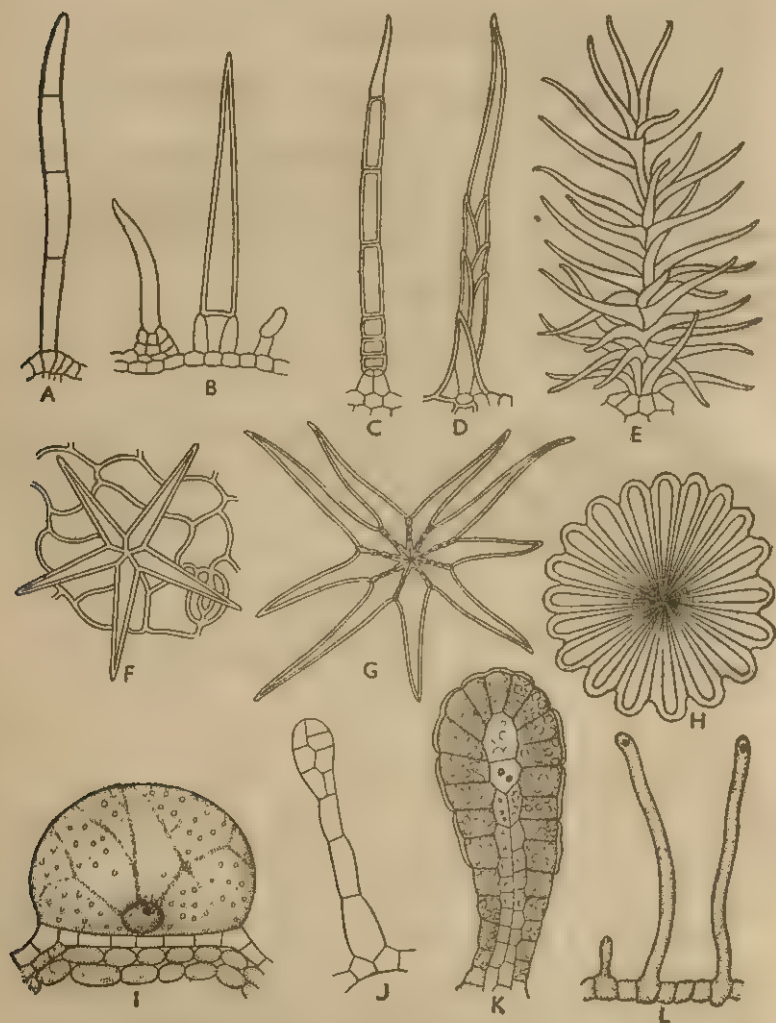


FIG. 290. EPIDERMAL OUTGROWTHS

A, ordinary hair of tobacco ; B, pointed hair of *Lantana* ; C, hair of sunflower ; D, hair of *Mimosa* ; E, dendroid hair of *Mimosa* ; F, stellate hair of *Althaea* ; G, same of *Sida* ; H, peltate hair of *Olea* ; I, water vesicle of *Mesembryanthemum* ; J, colleter of tobacco ; K, glandular trichome in the stipule of *Viola* ; L, root hair of pea.

cuticle) is formed as a result of metabolism of the epidermal cells.

The cuticle may be absent in cases, where the walls of the epidermal cells are very thin. The deposition of cutin takes place in varying degrees of proportion in plants living under different environmental conditions. For instance, plants growing under xerophytic conditions possess a thick, well-developed cuticle (e.g., *Agave*, *Aloe*, *Nerium*, etc.). In water plants, however, in case of submerged ones (e.g., *Vallisneria*, *Hydrilla*, etc.), silica deposition* takes the place of cutin; on the other hand, in case of floating ones (e.g., *Eichhornia*, *Limnanthemum*, *Nymphaea*, etc.), the dorsal surface is provided with a waxy coating. This coating does not allow any wetting of the surface. The inner walls of the

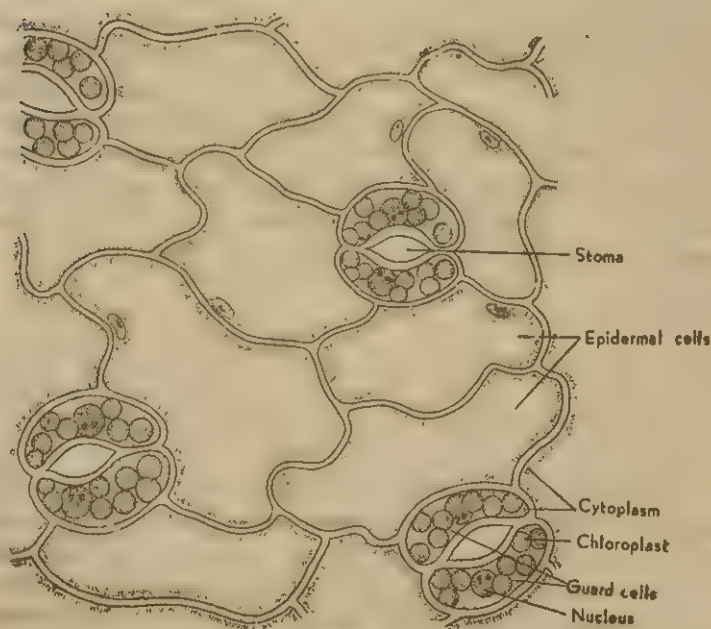


FIG. 291. STOMATA IN SURFACE VIEW
(Redrawn from Holman & Robbins).

epidermal cells firmly attach the epidermis with the sub-epidermal tissues.

The deposition of silica also takes place in some land plants, like members of the families Cyperaceae and Gramineae, as well as in *Equisetum*, a pteridophyte.

Two types of epidermis are frequently met with, **simple** and **multiple**. In the former case, the epidermis is single-layered,

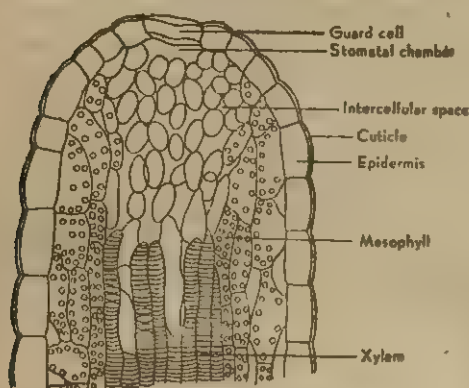


FIG. 292. HYDATHODE
(Modified after Haberlandt).

discussed in Chapters III and IV. The epidermal openings, comprising of **stomata** (Fig. 291) **water stomata**, and **hydatodes** (Fig. 292) have also been dealt with there.

as is found in the majority of plants. On the other hand, a multiple epidermis is one, which is made up of more than one layers of cells, commonly seen in *Nerium*, *Ficus*, *Eugenia*, *Agave*, *Aloe*, etc.

Of the epidermal outgrowths (Fig. 290), the **glands**, **hairs**, **scales**, and **water vesicles** have already been

B. THE PERIDERM

In the secondary plant body, the epidermis is replaced by the **periderm**. The periderm takes its origin either in the epidermis or in the sub-epidermal layers by the activity of the **phellogen** or **cork cambium**. On its outer face, this phellogen gives rise to the **phellem** or **cork cells**, which actually form the **dermis** or **skin** of the plant body; the **phelloderm** or **secondary cortex** is produced on the inner face (Fig. 273). In some plants like *Psidium*, *Eucalyptus*, *Acacia moniliformis*, etc., successive layers of periderm enclosing pockets of dead cortical or phloem tissues are formed and sloughed off as the **scale bark** or **rhytidome**. During leaf-fall, the periderm produces an **abscission layer** (Fig. 289) to seal the injured portion. Similarly, in the healing of wounds, a secondary cambial layer, formed in the cells lying adjacent to the injured ones, gives rise to the **callus** tissue, which

protects the exposed internal tissues from the attack of external agencies.

C. THE EXODERMIS

In case of roots, when the root hairs cease to function and wither away, the epiblemma as well as a few outer layers of the cortex become suberized and form a dead tissue, called the **exodermis**, which is well adapted as a protective coat.

II. THE MECHANICAL SYSTEM

Every plant, from the minutest micro-organism to the most highly developed tree, has to fight its way through adverse circumstances in order to maintain its normal life functions. One of the most important of all such adverse circumstances is the *mechanical injury* due to transverse or bending stresses, longitudinal pulls, longitudinal compressions, radial pressures and shearing stresses. In order to safeguard its organs against such injuries, a plant always develops some specialized groups of cells, which constitute the *mechanical tissues*.

The different organs in higher plants are subjected to different types of stresses, pulls, compressions, etc. Accordingly, the modes of distribution of the mechanical tissues in roots, stems, and leaves are also different. The specialized mechanical cells are called the **stereids**, and these collectively form the **mechanical system** or **stereome**.

THE MECHANICAL CELLS. The *collenchyma*, *sclerenchyma*, *phloem fibres*, and *xylem fibres* are the chief elements constituting the mechanical tissues. The collenchyma satisfies chiefly the mechanical requirements in the growing organs, while in mature regions the sclerenchyma, phloem fibres and xylem fibres afford the requisite mechanical strength or rigidity.

THE PRINCIPLES UNDERLYING THE DISTRIBUTION OF MECHANICAL TISSUES. In order to secure maximum strength with the minimum expenditure of material, four mechanical principles are followed in the construction of the plant organs.

(1) **Inflexibility.** Aerial parts of plants are constantly subjected to the bending strains in different planes. When a straight rod is bent, the convex side is lengthened and the concave

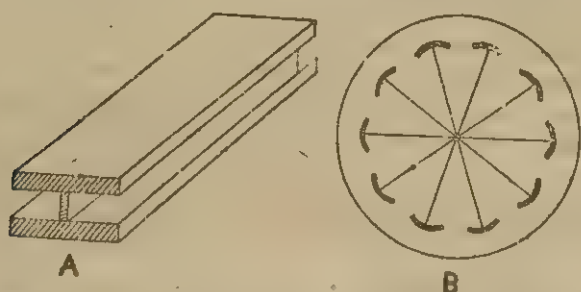


FIG. 293. I—GIRDERS

A, a single girder : B, system of girders in t.s. of a dicotyledonous stem.

side is shortened, but the centre is least affected, so the peripheral parts in plants are subjected to the greatest tension, which gradually decreases and finally falls to zero at the centre, which is known as the **neutral** or **null point**.

In cylindrical organs, in order to resist bending stresses in several directions at right angles to the longitudinal axis, mechanical tissues are arranged in one or more circles near the periphery, *i.e.*, many I-girders are so arranged, that they have a common neutral axis, and their flanges come in contact laterally forming a mechanical cylinder. A typical girder consists of two bars or *flanges* of mechanically effective material, joined together by a connecting piece or *web* (Fig. 293).

(2) **Inextensibility.** A resistance to longitudinal tension is best secured by the concentration of the resistant elements into a single, compact and cylindrical strand, the degree of resistance depending upon the cross-sectional area of the resistant elements. If many thinner strands were placed peripherally, a one-sided pull might rupture some of them more readily.

(3) **Incompressibility.** A resistance to a longitudinal compression is made by placing the mechanical tissues centrally, and to a radial pressure, by placing them at the peripheral shell. Both these are expressed in the structures of subterranean and submerged organs.

(4) **Shearing stresses.** A *shearing stress* is a mechanical force, which, when applied to a plant organ, causes or tends to cause the displacement of the particles of the said organ. On the other hand, the property of the organ (subjected to such a shearing stress) to resist is known as its **shearing resistance**.

DISTRIBUTION OF MECHANICAL TISSUES. Schwendener (1892) recognized *twenty-eight* different types of inflexible organs in the monocotyledons only, depending on the variation in the distribution of mechanical tissues in them. Of these, only a few cases, which may also fit in with the construction of the mechanical systems in some dicotyledonous plants as well, will be discussed here in brief.

(a) **In cylindrical organs.** The cylindrical organs are those, which are subjected to bending at any plane at right angles to the longitudinal axis ; such organs may or may not be strictly cylindrical, however, from the geometrical point of view.

(i) *Sub-epidermal girders.* In the stems of Labiatae, and in the inflorescence axes and petioles of Araceae, the mechanical tissues are arranged below the epidermis. The square stem of Labiatae is characterized by having two diagonally arranged collenchymatous girders, and this is regarded as the simplest type of mechanical construction in cylindrical organs (Fig. 294, A). In the petioles and inflorescence axes of the aroids, the fibrous strands of varying sizes are associated with the vascular bundles forming the sub-epidermal girders. (Fig. 294, B).

(ii) *Composite peripheral girders.* This system is common in the stems of Cyperaceae and Juncaginaceae. In the stems or haulms of *Trichophorum germanicum* (Fig. 294, C) the I-girders, mostly five or six in number, are arranged at regular intervals. The outer and the inner flanges abut on the two faces of a vascular bundle, which forms the web. In *Cyperus vegetus* (Fam. Cyperaceae) the two flanges, however, are widely separated from one another, and as such, the web is formed by the vascular bundle as well as the adjoining parenchyma (Fig. 294, D). A more complicated type is revealed in the stems of *Juncus glaucus* (Fam. Juncaginaceae). In this case (Fig. 295, A), in between the two flanges of the girder there lie the large vascular bundle, a small outer fibrous sheath, parenchyma cells, a large air-space and another patch of parenchyma.

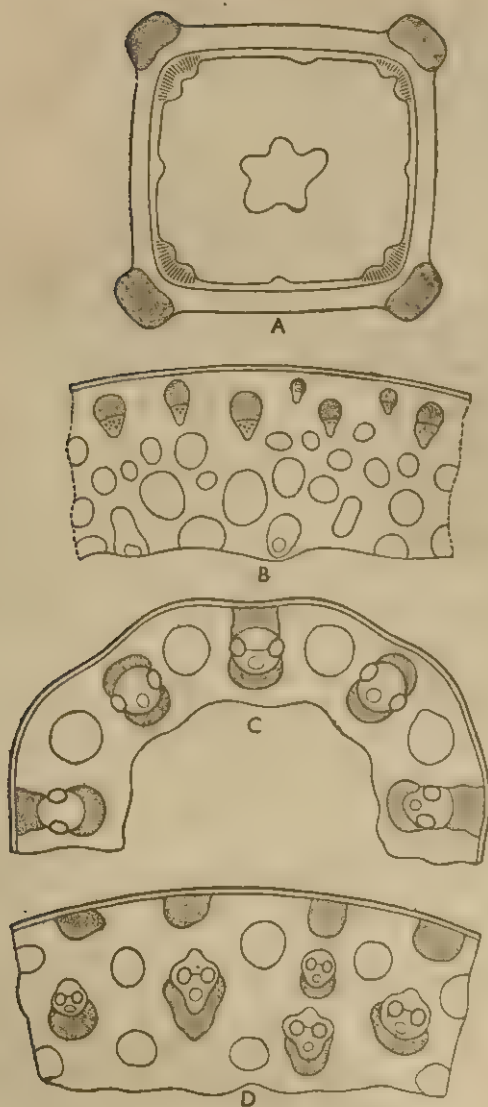


FIG. 294. DIAGRAMS SHOWING THE DISTRIBUTIONS OF MECHANICAL ELEMENTS

A, t.s. through an internode of *Lamium album* ;
 B, t.s. of petiole of *Colocasia antiquorum* ; C,
 t.s. of stem of *Trichophorum germanicum* ; D,
 t.s. through the haulm of *Cyperus vegetus*.

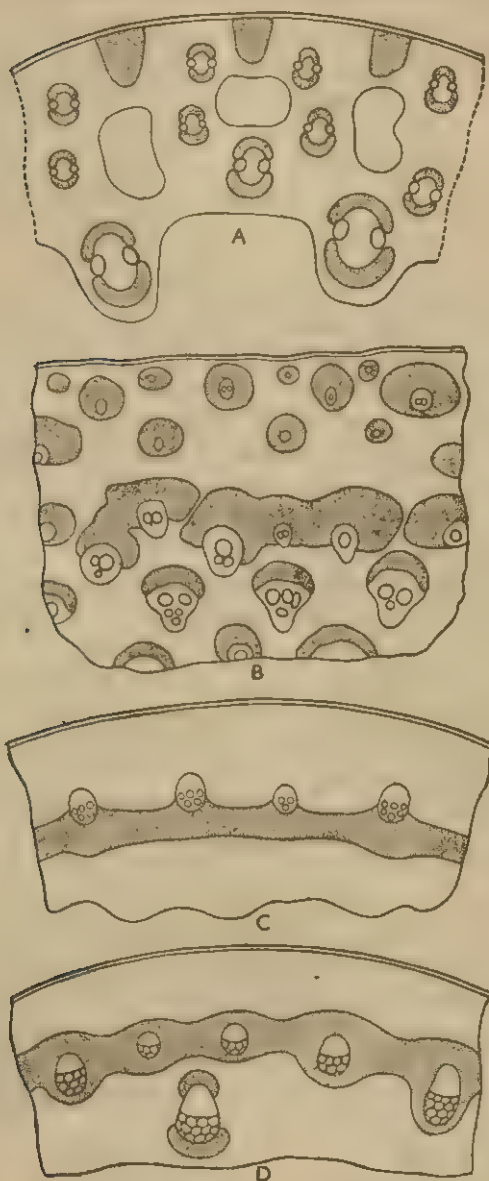


FIG. 295. DIAGRAMS SHOWING THE DISTRIBUTIONS OF MECHANICAL ELEMENTS (Contd.)

A, t.s. of stem of *Juncus glaucus*; B, t.s. of inflorescence axis of *Phoenix dactylifera*; C, t.s. of scape of *Allium odorum*; D, t.s. of stem of *Convallaria verticillata*.

(ii) *Sub-cortical fibro-vascular strands.* In this system, the fibrous bundles are shifted from the sub-epidermal region to the central position by the differentiation of parenchyma cells. In the stems and inflorescence axes of bamboos, palms, *etc.*, the bundle sheaths fuse laterally to give rise to an irregular ribbon-shaped strip, forming a hollow cylinder. The sheaths of the inner bundles, however, are poorly developed, and afford local rigidity only (Fig. 295, B).

(iv) *Simple hollow cylinder or tube of stereome with embedded vascular bundles.* The majority of the monocotyledonous plants show this type of arrangement. It is particularly noticed in the families like Liliaceae, Orchidaceae, Iridaceae, and Dioscoreaceae, and is also not infrequent among the dicotyledonous families like Chenopodiaceae, Caryophyllaceae, Cucurbitaceae, Geraniaceae, *etc.* In the stems of monocotyledons, the vascular bundles lie either in contact with the fibrous cylinder, or embedded in it (Fig. 295, C).

A series of transitional forms in between the extra-cambial to the intra-cambial mechanical cylinders can be found among the dicotyledons.

(v) *Peripheral hollow cylinder or tube of stereome strengthened further by isolated sub-epidermal girders.* The stems of some grasses show the presence of a tubular stereome with additional sub-epidermal girders lying at regular intervals. Here, the vascular bundles generally lie on the inner side of the mechanical cylinder, but they may also extend upto the centre of the stem. (Fig. 295, D).

(b) *In bilateral organs.* The leaves are the most important of all the bilateral organs among higher plants. The mechanical requirement of the leaf is satisfied by arranging the I-girders in a parallel series at right angles to its longitudinal axis.

In the simplest cases like *Typha*, *Musa* (Fig. 296, A) *Pandanus*, *Carex* (Fig. 296, B) and grasses, the sub-epidermal I-girders extend from the upper to the lower face of the leaf. The two flanges are made up of sclerenchyma, and the web of either the vascular bundle alone or the bundle and the associated parenchyma.

In more complicated cases, as in the leaves of *Saccharum*, *Zea* (Fig. 296, C), *Phoenix*, *etc.*, the fibrous strands are irregularly distributed on the two faces. In this type, broad sub-epidermal

mechanical plates, composed of sclerenchyma cells, are placed towards the upper face, while towards the lower one there are a number of small ordinary girders, placed side by side.

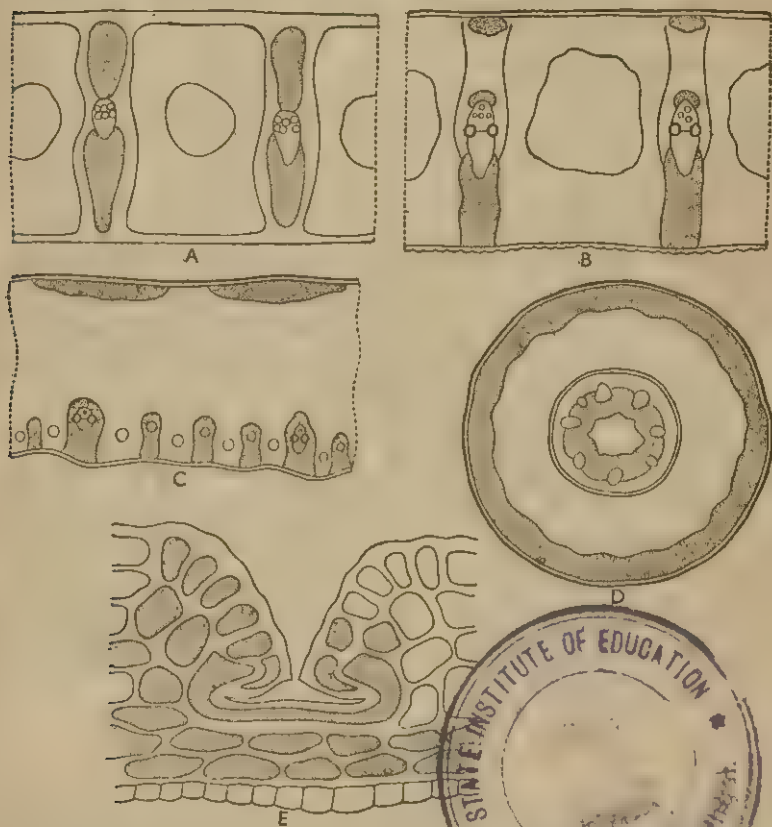


FIG. 296. DIAGRAMS SHOWING THE DISTRIBUTIONS OF MECHANICAL ELEMENTS (Contd.)

A, t.s. of leaf of *Musa* ; B, t.s. of leaf of *Carex* ; C, t.s. of leaf of *Zea mays* ; D, t.s. of root of *Zea mays* ; E, t.s. through the commissural region of the leaves of *Equisetum*.

(c) In inextensible organs. All the anchoring organs of plants, particularly the roots, are the best examples of inextensible organs, which are subjected to longitudinal tensions. In the roots, the mechanical elements lie associated with the conducting tissues at the centre (Fig. 296, D) ; this offers a resistance to the upward

pull. The twining and submerged stems are also more or less similarly constructed.

(d) **In incompressible organs.** The inextensible organs are not only subjected to an upward pull, but are liable also to the radial pressure and longitudinal compression. The radial pressure is, however, averted with the development of a firm peripheral shell, made up of fibres. To withstand longitudinal compression, the organs develop the stereome in the same fashion as in inflexible organs.

(e) **To offer resistance to shearing stresses.** In leaves, fluttering in the wind tends to cause laceration of the margins, and this is overcome by the thickening of the epidermal walls, as well as by coenchymatous or sclerenchymatous subepidermal cells, as found in the aroids and pine respectively. In the absence of a necessary protection, as in the banana leaf, the lamina is very easily torn to pieces.

When additional strength is necessary, as in the date palm leaf, the sclerenchyma sheaths (which are thicker towards the two faces) of the series of parallel vascular bundles, small and large, form a series of parallel I-girders with flanges nearest the faces to add to their inflexibility.

In leaves of *Equisetum*, at the commissural regions a special type of mechanical cell, the **clamp cell**, is found, which helps to prevent the tearing of the leaves (Fig. 296, E).

III. THE PHOTOSYNTHETIC SYSTEM

It is well known that all green plants can prepare their own carbohydrate food from carbon dioxide and water with the help of chloroplasts in presence of sunlight. This process is known as **photosynthesis**. The organ as well as the environmental factors influencing photosynthesis come within the scope of this system.

THE PHOTOSYNTHETIC CELLS

In some primitive algae, the entire body of the organism acts as the photosynthetic organ, and the **chlorophyll**, the photo-

synthetic pigment, remains in a diffused condition throughout the protoplast. In others, which are more highly organized, the chlorophyll is located inside a particular structure, known as the **chloroplast**. In higher plants, the photosynthetic cells remain confined to the green parts only, like leaves, primary and herbaceous stems, phylloclades and cladodes, etc. In dorsiventral leaves, two types of photosynthetic cells are met with (Fig. 297). The cells lying below the upper epidermis constitute the **palisade parenchyma**. The cylindrical cells in this region

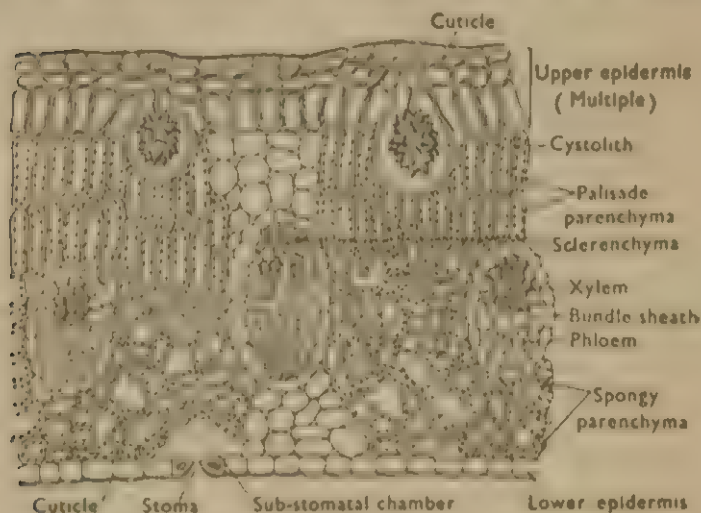


FIG. 297 T.S. OF INDIA RUBBER LEAF (in part)

lie compacted together at right angles to the cells of the upper epidermis, contain abundant chloroplasts, and have little or no intercellular spaces. Lying below the palisade and extending up to the lower epidermis is the **spongy parenchyma**, whose cells are isodiametric, loosely arranged with prominent intercellular spaces and air chambers, and containing a lesser number of chloroplasts. Sometimes, the cells of the palisade parenchyma become much branched taking the shapes of extended arms, and these are known as the **arm-palisade cells**.

The origin, structure and function of chloroplasts have been previously discussed in Chapter III.

The palisade parenchyma forms the main photosynthetic tissue. Consequently, the greater is the surface of the palisade tissue, the greater is the amount of photosynthesis. An interesting case of expansion of the photosynthetic area within the compass of a very limited space is afforded by the photosynthetic cells of the pine needle. Here the walls of these cells are peculiarly folded or projected inside the cell cavities in order to present a greater surface for photosynthesis in relation to the narrow needle-shaped leaves. For an uninterrupted and continuous photosynthesis the prepared food, however, must be quickly removed from its seat of formation. This is Haberlandt's 'principle of expeditious translocation.' This principle is dependent to a great extent upon the mode of construction of the photosynthetic system with regard to the different types of leaves.

Light plays a very important role in the organization and distribution of the photosynthetic system. There are some plants, which favour the shade with a lesser intensity of illumination than others for carrying on effective photosynthesis. In every case, however, the photosynthetic system is situated near the periphery for obtaining the maximum amount of light.

IV. THE VENTILATING SYSTEM

The living plants exhibit an interchange of gases like oxygen, carbon dioxide, hydrogen, or sulphurated hydrogen, as well as water vapour and volatile vegetable oils with the surrounding atmosphere. This interchange is dependent on the surface area of the plant organ through which diffusion takes place, and is directly proportional to it. The individual cells or the plant organs, internal as well as external, which take part in the gaseous exchange, together constitute the **ventilating or aerating system**. The following organs form this system : (a) cuticle, (b) stomata, (c) lenticels, (d) ventilating spaces and tissues, and (e) **pneumatophores**.

It has been proved experimentally that cuticular diffusion takes place from the aerial organs of plants. This type of diffusion is, however, very negligible in comparison to that taking

place through stomata, lenticels, and pneumatophores. The structure of stomata and lenticels have already been discussed previously.

The plants growing in the estuarine areas often possess **pneumatophores**. These are negatively geotropically growing roots, which come up into the air, and are provided with pores (**pneumathodes**) over the surface (Fig. 298). The inner parenchyma consists of prominent air spaces (Fig. 299), and is termed **aerenchyma**. Sometimes, the epidermis (epiblema) of these breathing roots is thrown off, and the aerenchyma gets directly exposed to the air.

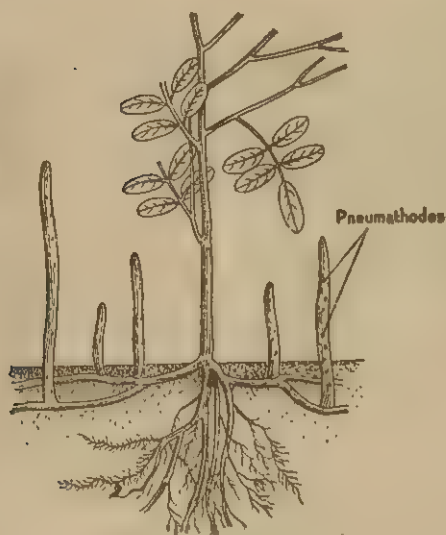


FIG. 298. BREATHING ROOTS OF
Ceriops roxburghiana.

Pneumathodes also occur on the aerial roots of orchids. These appear as distinct white spots on the outer surfaces to the naked eye, and are, in reality, portions of the velamen saturated with water.

The cells, which are responsible for aeration, always remain in contact with conspicuous inter-cellular air spaces. The extent and distribution of the ventilating spaces vary to a great degree according to the needs and functions of the different tissue systems. The ventilating spaces consist of elongated passages, wide cavities, narrow clefts and interstices. Of these, the former two occur in the mesophyll of leaves, in the stems and petioles of submerged plants, and in the breathing roots. The ventilating clefts are found in the leaves of many members of Fam. Myrtaceae, where they are formed between the cells,

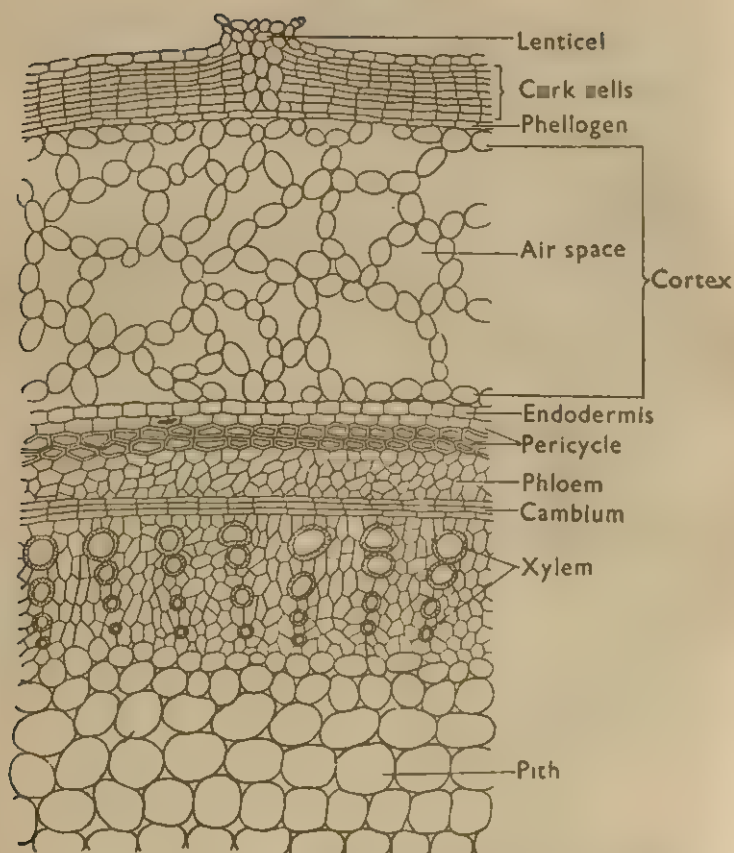


FIG. 299. T. S. OF BREATHING ROOT OF *Ceriops* (in part)

passages or cavities, or they separate as different sheets or layers of cells.

PART III
**EMBRYOLOGY
AND CYTOLOGY**



EMBRYOLOGY

INTRODUCTORY CHAPTER

The immortal Greek philosopher, Aristotle, is customarily looked upon as the father of the study of natural sciences. It is interesting, however, that there are reasons to believe that he did not recognize sexuality in plants. Theophrastus in the third century B.C., and about three hundred years later, Pliny simply referred to the male and female date palms, but even these references were not made on their personal observations. This state of affairs continued upto the sixteenth century. It was Nehemiah Grew, who in 1682, first clearly stated that the stamens were nothing but the male organs of a plant. R. J. Camerarius (1694) suggested from his studies that the anthers are the male sex organs of a plant, while the ovaries-with the styles were the female ones. His idea was fully confirmed by J. G. Kölreuter in 1761. For our knowledge regarding the nature and development of male and female gametophytes in angiosperms, we are indebted to workers like Amici, Hofmeister, Hartig, Reichenback, Strasburger, Warming, Fischer, Guignard, and others.

The phenomenon of syngamy was first discovered in *Monotropa hypopitys* by Strasburger in 1884, and Nawaschin (1898) established the phenomenon of double fertilization from his studies on *Lilium martagon* and *Fritillaria tenella*. It is interesting to note, however, that the question of embryogeny was first studied in detail by Hanstein in 1870 in *Capsella* and *Alisma*, though he had no clear idea about syngamy at that time.

During the twentieth century, a remarkable progress has been made in the field of embryology. The pioneer workers like Schnarf, Soueges, Finn, Murbeck, Rosenberg, Juel, Fagerlind, Gustafsson, Chiarugi, Ernst, Wulff, Coulter, Johnson, and others have made valuable contributions in this field of study. In our country, the works of Maheshwari, Banerji, Swamy, and others are worth mentioning. All the modern workers are particularly keen about throwing some light on the importance of embryology in relation to taxonomy.

CHAPTER I

DEVELOPMENT OF THE GAMETOPHYTES

DEVELOPMENT OF THE MALE GAMETOPHYTE (Figs. 300-301).

The stamen usually arises as a semi-lunar papillate projection on the floral axis. The anther is formed early in the life of the organ, the filament being a later development, so that, in young flower buds the anther is well-developed, while the stalk is not yet formed. The sporangia are eusporangiate, *i.e.*, these originate from a group of several cells. In the normal four-celled anther, the sporogenous tissue is developed at each of the four corners of the young anther.

On making a cross section of a very young anther, in the early stage of its development in the primordium, masses of cells with large size, denser cytoplasmic contents, and large nuclei will be noted in the centre of each of its four angles. These cells constitute the **archesporium**. The archesporial cells become enlarged in the radial direction and divide periclinally, forming two layers of cells. The outer layer is called the **tapetum** (a nutritive tissue, supplying food to the developing pollen grains), while the inner one forms the layer of **primary sporogenous cells**. The tissues lying outside the archesporium give rise to the anther wall, which consists, usually, of *three* different zones in succession (from outside inwards), namely, the single-layered **epidermis**, the solitary **fibrous layer***, and one or more **parietal** or **wall layers**. The primary sporogenous cells may either behave directly as **pollen mother-cells (microspore mother-cells)**, or may divide giving rise to daughter cells, which then act as spore mother-cells. In case where the primary sporogenous cells undergo division, the tapetal cells may also divide forming a tapetal sheath. Each pollen mother-cell divides meiotically and usually produces *four pollen grains (microspores)*. In some cases, the number of pollen grains produced from each pollen mother-cell may be

* In anthers having valvular or porous dehiscence, the fibrous layer is usually either not developed at all, or developed very feebly,

more than four (**polyspory**) or less, due to irregular or incomplete divisions. With advancement in age, the walls of the cells of the fibrous layer become lignified or suberized with thin original

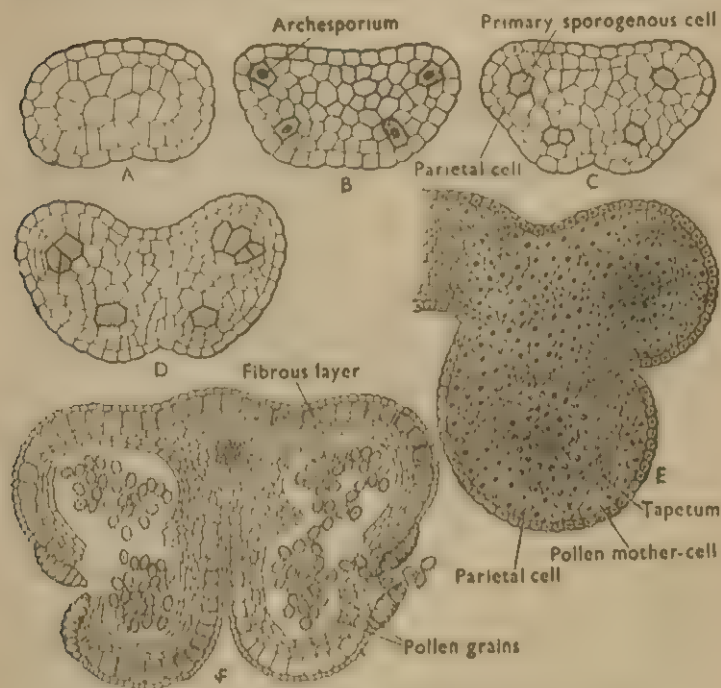


FIG. 300. A -F, STAGES IN THE DEVELOPMENT OF ANTHER AND POLLEN GRAINS.

cellulosic walls here and there. As a result of drying, these thick and thin areas on the walls undergo unequal shrinkage, causing the anther wall to get reaptured. Consequently, the pollen grains are liberated.

A pollen grain germinates only when it has attained full maturity. The pollen grain, on germination, gives rise to a **pollen tube**, which is regarded as the male gametophyte. Thus, the pollen grain is the first cell of the male gametophytic generation. It is interesting to note that the male gametophyte develops remarkably uniformly throughout the angiosperms.

Before germination, it increases considerably both in size as well as in volume ; a conspicuous central vacuole appears in the midst of the dense cytoplasm, thereby shifting the position of the nucleus from the central to a peripheral one. The first

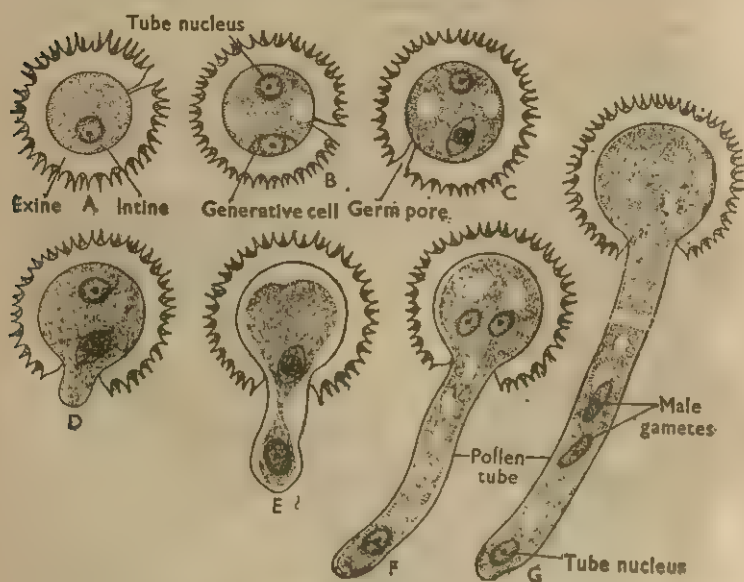


FIG. 301. GERMINATION OF POLLEN GRAIN AND DEVELOPMENT OF THE POLLEN TUBE.

stage in the germination is marked by the formation of a small, nucleated cell lying against the spore wall. This small cell, the **generative cell**, is separated from the rest of the large, naked cell, the **vegetative** or **tube cell**, by means of a distinct wall. Further, the nuclei of these two cells also differ from one another in size, structure and staining qualities ; the nucleus, of the vegetative cell possesses a very prominent nucleolus, while that of the generative cell may have a small one or none at all. Very soon, the generative cell gets itself detached from the spore wall, becomes fusiform or ellipsoid in shape, and remains embedded in the cytoplasm of the vegetative cell. Subsequently, the generative cell divides and gives rise to two distinctly walled lenticular, ellipsoid, vermiform, or spherical cells (not naked nuclei, as previously believed), the **male gametes**. These two gametes

are usually identical in shape and size, but, during their course of downward journey through the pollen tube, their shape may undergo some change. It should be noted, however, that this division of the generative cell may take place either within the original spore wall or within the pollen tube. The nucleus of the vegetative cell, commonly referred to as the **tube nucleus**, usually shows sign of degeneration with the maturation of the generative cell. Finally, it may remain within the spore wall, or may enter the pollen tube sooner or later, or even may be completely degenerated.

Earlier workers considered the tube nucleus to be of great significance in directing the course of growth of the pollen tube, as it usually occupies a distal position within the tube. Recent workers, like Poddubnaja-Arnoldi, Suita and others, however, do not share this opinion. On the contrary, they consider the tube nucleus as purely a non-functional vestigial structure, on the following grounds.:

(a) The tube nucleus does not necessarily occupy a position at the distal end of the growing pollen tube, but lies, in many cases, behind the male gametes.

(b) In case of branched pollen tubes, only one of the branches contains the tube nucleus, but all of them can grow quite satisfactorily.

(c) In some plants, the growing pollen tube does not contain any tube nucleus, because it has undergone degeneration prior to the formation of the pollen tube.

DEVELOPMENT OF THE FEMALE GAMETOPHYTE (Figs. 302—303)

The ovule arises as a several-celled placental outgrowth including the epidermis and a few cells of the hypodermis. This, later on, gives rise to the nucellus, from the basal part of which one or two integuments arise. In cases of ovules having two integuments, the inner one is usually formed first, and is more delicate and inconspicuously developed than the outer one. Early during the development of an ovule, the **archesporium** is differentiated as a single or a few hypodermal cells (distinguished from their neighbouring cells by their bigger size, more abun-

dance of cytoplasm and conspicuous nuclei). In the crassinucellate ovules, the cells of the archesporium divide, mainly periclinally, and give rise to the inner **sporogenous cells**, and the outer **primary parietal cells**. One or more of these sporogenous cells function as **megaspore mother-cells**. In the tenuinucellate ovules, on the other hand, the archesporium usually consists of the single terminal cell of an axial row of cells, produced on the middle row of the nucellus. This solitary cell, generally, becomes the sporogenous one later on, and behaves as the megaspore mother-cell.

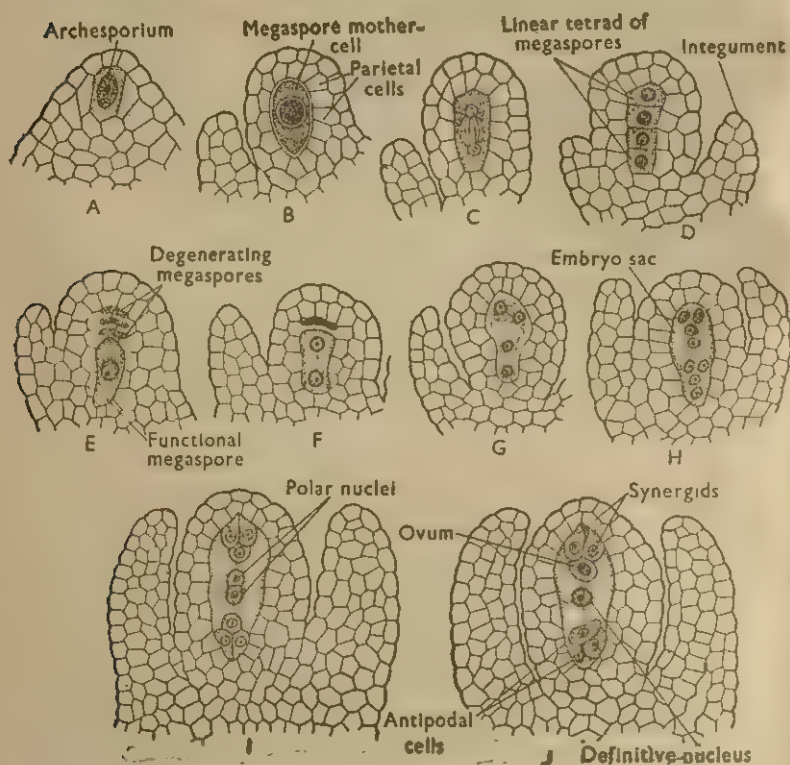


FIG. 302. GRADUAL STAGES IN THE FORMATION AND DEVELOPMENT OF THE EMBRYO SAC IN A CRASSINUCELLATE OVULE.

Next, reduction division takes place in the megaspore mother-cell, and as a result, a tetrad of megaspores is formed ; the megaspores usually lie in an axial row of four cells

(linear tetrad), of which the innermost one remains functional, while the other three degenerate and are left behind as black

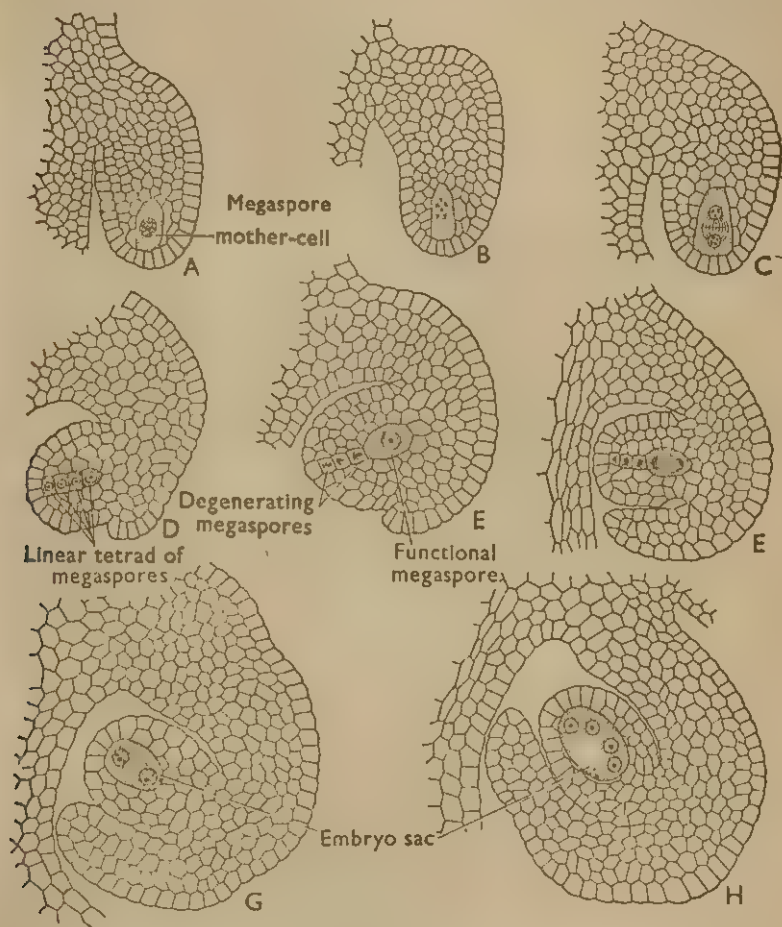


FIG. 303. GRADUAL STAGES IN THE FORMATION AND DEVELOPMENT OF THE EMBRYO SAC IN A TENUINUCELLATE OVULE.

scars for sometime. The functional megaspore then begins to enlarge at the expense of the tapetum and the nucellus, and forms the **embryo sac**, which is the female gametophyte. Initially each embryo sac is uninucleate. When it attains

maturity, changes take place in it, and the nucleus divides by three successive karyokinetic divisions into eight nuclei, of which four at first remain towards the micropylar end, and the other four towards the chalazal end. One nucleus

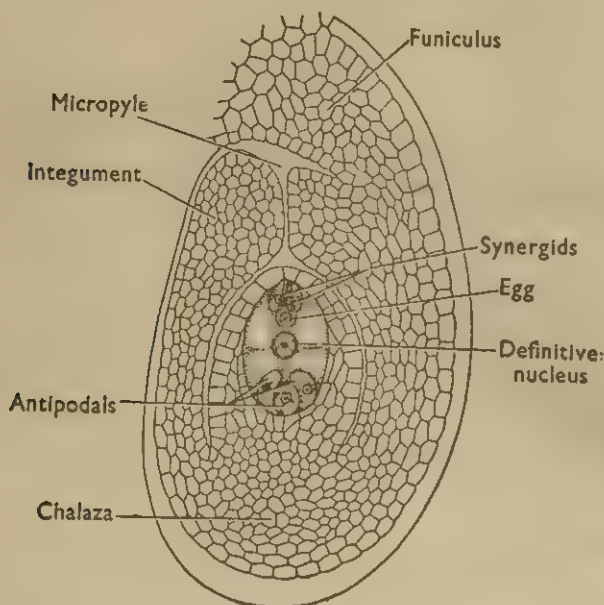


FIG. 304. MEDIAN LONGITUDINAL SECTION THROUGH AN OVULE SHOWING THE MATURE EMBRYO SAC READY FOR FERTILIZATION.

from each end then travels towards the centre and form a pair of **polar nuclei** (one *micropylar polar* and the other *antipodal polar*), which may or may not fuse to form the **definitive nucleus**. The remaining three nuclei at the micropylar end collectively form the **egg apparatus**, and the other three at the chalazal end also collectively constitute the **antipodals**. The mature egg apparatus consists of a central cell, the **egg** or **ososphere** or **ovum**, and two **synergids** or helping cells, one on each side of the egg. This is the condition of the mature embryo sac ready for fertilization (Fig. 304).

Thus, it is noted that in the **normal** or **ordinary type** (also known as the **Polygonum type**) of embryo sac development, five successive nuclear divisions take place in the formation of the

ovum. Furthermore, here the embryo sac (female gametophyte) is the product of a single megaspore only. Many deviations, however, from this type are found in the various members of the angiosperms. A brief account of the more important ones is given below (Fig. 305).

Oenothera type. In *Oenothera* and certain other members of the Fam. Onagraceae, the usual linear tetrad of megaspores is formed, but normally the outermost megaspore, instead of the innermost one, gives rise to the embryo sac. In this case, only four successive nuclear divisions interpose in between the megaspore mother-cell and the ovum. The functional megaspore nucleus first divides into two, both remaining at the micropylar end, and a vacuole appears below them. Each of these nuclei divides again and out of the four nuclei formed, three organize the egg apparatus and the fourth one is converted into a polar nucleus. There is neither a second polar nucleus, nor are there the antipodals.

Allium type. This type of embryo sac is found in *Allium* and a few genera like *Scilla*, *Trillium* and others of the Fam. Liliaceae, as well as in many other genera belonging to a large number of families of angiosperms. The megaspore mother-cell divides and forms two cells, the upper one degenerating quickly. The nucleus of the lower cell then undergoes three successive divisions, and ultimately gives rise to the usual octonucleate type of embryo sac. It should be noted, however, that there are only four nuclear divisions intervening between the megaspore mother-cell and the ovum. Further, two megaspore nuclei take part, in this case, in the formation of the embryo sac.

Peperomia type. In the genus *Peperomia* (Fam. Piperaceae) all the four megaspore nuclei take part in the formation of the embryo sac. The four megaspore nuclei, produced from the megaspore mother-cell, remain arranged crosswise with a vacuole between them, but without any wall. Sixteen free nuclei are formed from them, as a result of two successive nuclear divisions. The arrangements of these nuclei vary from species to species. The egg apparatus is made up of a single synergid and an ovum only, while the fusion nucleus is formed by the union of eight nuclei and six degenerating (in *P. pellucida*), or by the union of all the other fourteen nuclei (in *P. hispidula*).

A large number of variations of this type can be seen in some other families. In some species of the genus *Euphorbia* (Fam. Euphorbiaceae), and in the Fam. Penaceae, the sixteen free nuclei produced become arranged into four groups, each group containing four nuclei. One nucleus out of each such group behaves as a polar nucleus, while the other three nuclei become organized into groups of cells. The four polar nuclei undergo fusion, while the three cells towards the micropylar end of the embryo sac form the egg apparatus; other cells ultimately degenerate. In *Gunnera* (Fam. Haloragidaceae), three nuclei form the egg apparatus, seven give rise to the fusion nucleus, while six undergo degeneration.

Drusa type. This type of embryo sac development is noted in the type species *Drusa oppositifolia* (Fam. Umbelliferae). It is also found in a number of species of several other genera like *Rubia* (Fam. Rubiaceae), *Ulmus* (Fam. Ulmaceae), *Chrysanthemum* (Fam. Compositae), and others. In this case, out of the four megaspore nuclei, only one remains at the micropylar end, while the remaining three go towards the chalazal end. Now, two successive nuclear divisions result in four micropylar nuclei and twelve antipodal ones. From each of the two groups of nuclei, one nucleus travels to the centre to form a pair of polar nuclei. As a result, a mature embryo sac consists of three nuclei at the micropylar end (one of which forms the ovum), two at the centre and eleven at the chalazal end.

Fritillaria type. In *Fritillaria*, *Lilium*, *Tulipa* and some other members of the Fam. Liliaceae, as well as in some genera of a few other families of angiosperms, walls are not formed in between the linear tetrad of megaspore nuclei. With the development of the embryo sac, only one megaspore nucleus remains towards the micropylar end, while, the other three travel towards the chalazal end. All the four nuclei then begin to divide, but before the completion of the division, the chalazal group of nuclei fuse. Consequently, another four-nucleate stage becomes evident for the second time. Of these, two are micropylar and two are chalazal in position, and they remain separated by a prominent vacuole. It should be noted that the former (micropylar) nuclei are haploid, while the latter (chalazal) ones are triploid.

Subsequent to this, another free nuclear division takes place resulting in eight nuclei in two groups. The upper group

| Type | Megaspore mother-cell | Divisions | | | | | Mature embryo-sac |
|--|-----------------------|-----------|----|-----|----|---|-------------------|
| | | I | II | III | IV | V | |
| <u>Polygonum</u> (Ordinary) Monosporic 8-nucleate | | | | | | | |
| <u>Oenothera</u> Monosporic 4-nucleate | | | | | | | |
| <u>Allium</u> Bisporic 8-nucleate | | | | | | | |
| <u>Peperomia</u> Tetrasporic 16-nucleate | | | | | | | |
| <u>Penaea</u> Tetrasporic 16-nucleate | | | | | | | |
| <u>Drusa</u> Tetrasporic 16-nucleate | | | | | | | |
| <u>Fritillaria</u> Tetrasporic 8-nucleate | | | | | | | |
| <u>Plumbagella</u> Tetrasporic 8-nucleate | | | | | | | |
| <u>Plumbago</u> Tetrasporic 8-nucleate | | | | | | | |
| <u>Adoxa</u> Tetrasporic 8-nucleate | | | | | | | |

FIG 305. DIAGRAMMATIC REPRESENTATIONS OF THE STAGES IN THE DEVELOPMENT OF THE DIFFERENT TYPES OF EMBRYO SAC.

comprises of the ovum, two synergids and a haploid polar

nucleus, and from the lower group are formed the three antipodals and a triploid polar nucleus. In some cases, only two antipodals are developed.

Plumbagella type. The mode of development of the embryo sac in *Plumbagella* (Fam. Plumbaginaceae) is to some extent similar to that of *Fritillaria*. The four megaspore nuclei remain free and naked within the cavity of the embryo sac. One nucleus is found at the micropylar end, while the other three migrate towards the chalazal end and fuse there. Both the nuclei then divide, and the embryo sac normally becomes four-nucleate, two of which are haploid and two triploid. One of these haploid nuclei forms the ovum, and the other unites with one of the triploid nuclei to give rise to the fusion nucleus. The solitary antipodal cell is organized from the remaining triploid nucleus.

Plumbago type. In *Plumbago* and some other genera of Fam. Plumbaginaceae, the four megaspore nuclei, formed from the megaspore mother-cell, remain arranged crosswise, as in the *Peperomia* type. Each of these four nuclei then divides once again giving rise to four groups of paired nuclei. One nucleus from each group functions as a polar nucleus. The remaining nucleus of the micropylar pair organizes the ovum, while the rest disintegrate. Consequently, the mature embryo sac consists of only two nuclei, the haploid one of the ovum and the tetraploid one of the fusion nucleus.

Adoxa type. Another type of embryo sac development is found in *Adoxa* and *Sambucus* of the Fam. Caprifoliaceae. Though this type of development has been reported to take place in a number of genera belonging to various families of angiosperms, yet a large number of cases are doubtful. In *Adoxa*, the megaspore mother-cell divides twice to give rise to four megaspore nuclei, but no wall-formation takes place in between them. These four nuclei divide once again, and an octonucleate embryo sac is formed. Thus, in this case, only three successive divisions intervene between the megaspore mother-cell and the ovum, and all the four megaspore nuclei take part in the formation of the embryo sac. A mature embryo sac has the normal or ordinary type of organization.

From the above descriptions it is clear that the embryo sacs can be classified into different categories, depending on the number of

megaspores taking part in the formation of the embryo sac and the total number of nuclei present in it. When only one megaspore, out of a tetrad formed from a megaspore mother-cell, develops into an embryo sac, it is called a **monosporic sac**. This occurs probably in the majority of species. On the other hand, in some cases, the megaspore mother-cell divides only once forming a diad of megaspores, either the lower or the upper one of which forms the embryo sac ; such a type is known as the **bisporic sac**, as is found in *Allium*, *Scilla* (Fam. Liliaceae), and some members of Orchidaceae, Alismataceae, Butomaceae, Loranthaceae, Balanophoraceae, Podostemaceae, etc. In a few genera belonging to different families, the megaspore mother-cell does not undergo any division at all, but its nucleus divides several times, and ultimately it itself gives rise to the embryo sac, which is known as the **tetrasporic sac**.

CHAPTER II

DEVELOPMENT OF THE EMBRYO

FORMATION OF THE EMBRYO

It has already been described that fertilization takes place as a result of union between a male gamete and the egg (Fig. 306). After fertilization, the fertilized egg soon surrounds itself with a cellulose wall. As a result of fertilization, a stimulus of growth causes its rapid enlargement due to the continued cell divisions, ultimately forming a complete embryo within the ovule.

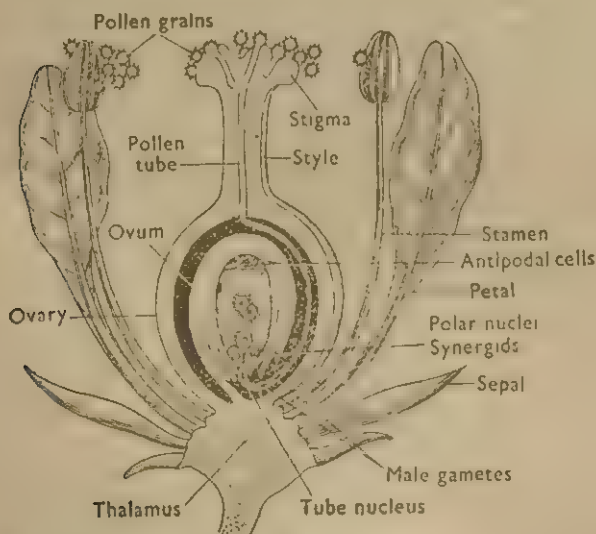


FIG. 306. LONGITUDINAL SECTION OF A FLOWER SHOWING THE PROCESS OF FERTILIZATION (*Semi-diagrammatic*).

Among the angiosperms, Johansen (1950) recognizes *six* different embryological types. Of these, in the **Piperad** type, the first division of the oospore is longitudinal, while in the five other types, the division is transverse. In the **Onagrad** and **Asterad** types, the apical cell, produced as a result of this transverse division of the oospore, divides longitudinally. On the other hand, this apical

cell in the **Caryophyllad**, **Solanad**, and **Chenopodiad** types divides transversely.

Schematically, the *six* types of Johansen can be represented as follows :

I. THE FIRST DIVISION OF THE OOSPORE LONGITUDINAL

PIPERAD TYPE. (e.g., *Peperomia* of Fam. Piperaceae, *Balanophora* of Fam. Balanophoraceae, and *Scabiosa* of Fam. Compositae).

II. THE FIRST DIVISION OF THE OOSPORE TRANSVERSE

A. *The division of the apical cell (in the second generation of cells) longitudinal.*

ONAGRAD TYPE. The basal cell, practically speaking, takes no part in the formation of the embryo. Examples are the members of Fam. Onagraceae, *Capsella* of Fam. Cruciferae, *Euphorbia* of Fam. Euphorbiaceae, *Trifolium* of S.F. Papilionaceae (Fam. Leguminosae), *Veronica* of Fam. Verbenaceae, *Lythrum* of Fam. Lythraceae, *Mentha* of Fam. Labiatae, *Juncus* of Fam. Juncaceae, *Lilium* of Fam. Liliaceae, and a number of other genera.

ASTERAD TYPE. The basal cell is responsible for the formation of the embryo. Examples are almost all the members of Fam. Compositae, *Polygonum* of Fam. Polygonaceae, *Erodium* of Fam. Geraniaceae, *Urtica* of Fam. Urticaceae, *Oxalis* of Fam. Oxalidaceae, *Lamium* of Fam. Labiatae, and *Poa* of Fam. Gramineae.

B. *The division of the apical cell (in the second generation of cells) transverse.*

(i) The basal cell, practically speaking, takes no part in the formation of the embryo.

CARYOPHYLLAD TYPE. The basal cell generally gives rise to the single-celled large suspensor. Examples are *Sagina* of Fam. Caryophyllaceae, *Medicago* of S.F. Papilionaceae (Fam. Leguminosae), *Corydalis* of Fam. Papaveraceae, *Myriophyllum* of Fam. Haloragidaceae, *Drosera* of Fam. Droseraceae, *Sagittaria* of Fam. Alismataceae, *Ruppia* and *Zannichellia* of Fam. Potamogetonaceae, and some others.

SOLANAD TYPE. The basal cell gives rise to a two- or more-celled suspensor. Examples are *Datura*, *Nicotiana*, *Physalis* and *Hyoscyamus* of Fam. Solanaceae, *Hydnora* of Fam. Hydnoraceae, *Linum* of Fam. Linaceae, *Sherardia* of Fam. Rubiaceae, *Papaver* of Fam. Papaveraceae, etc.

(ii) The basal cell is responsible for the formation of the embryo.

CHENOPODIAD TYPE. Examples are *Chenopodium* and *Beta* of Fam. Chenopodiaceae, *Myosotis* of Fam. Boraginaceae, and *Polemonium* of Fam. Polemoniaceae.

DEVELOPMENT OF THE EMBRYO

A. DICOTYLEDONOUS EMBRYO (Fig. 307)

The process of development of the embryo from the zygote in case of dicotyledons has been illustrated below from the classical example of the shepherd's purse (*Capsella bursa-pastoris*) of Fam. Cruciferae. The longitudinal section of a just-fertilized campylotropous ovule of this plant reveals the presence of a curved embryo sac within it, the zygote being situated facing the micropyle.

The first division of the zygote takes place by a wall transverse to the long axis of the ovule. Two or three early parallel divisions follow each other in rapid successions, giving rise to a small filament of usually 3-5 undifferentiated cells, called the **pro-embryo**. The basal cell of this filament towards the micropyle is the largest, and oval in shape, which attaches the pro-embryo to the wall of the embryo sac at the micropylar region. The cell at the opposite end, which is directed towards the interior of the ovule, enlarges, becomes spherical and constitutes the important **embryo cell**, from which the whole of the embryo (with the exception of the root tip) is formed. The remaining portion of the pro-embryo below the embryonic cell (including the basal cell) is called the **suspensor**. By further parallel divisions of the suspensor cells, the embryo cell is gradually pushed into the interior of the embryo sac. The further divisions of the suspensor cells are more or less regular. The first division of the embryo cell is median or longitudinal, i.e., parallel to the long axis of the filament, giving rise to two cells. The second division is also longitudinal, but the two walls

intersect with each other at right angles ; by the formation of a third wall the vertical cells are cut transversely and equally, forming eight equal-sized cells, called the **octants**. The terminal or outer four cells of the octants, by further divisions, grow out in a bilobed manner forming two lateral **cotyledons**, which are

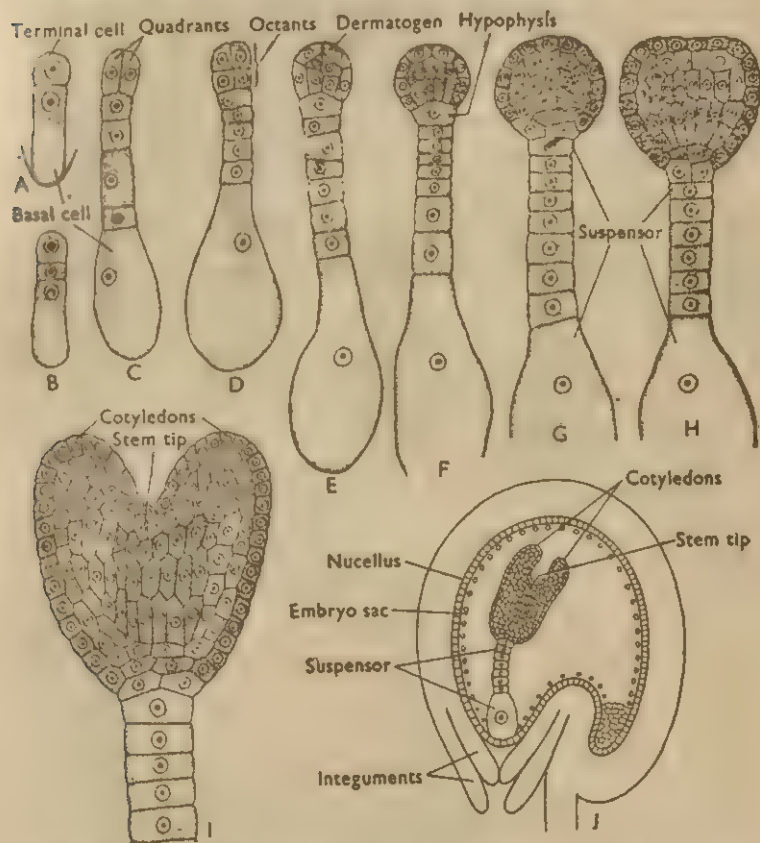


FIG. 307. GRADUAL STAGES IN THE DEVELOPMENT OF THE EMBRYO IN *Capsella bursa-pastoris*.

characteristic of dicotyledonous plants. From the depression situated between the two cotyledons a small protuberance of tissue develops, which forms the **plumule**. The four inner cells of the octants towards the suspensor form the **hypocotyl** and the **radicle** of the embryo. The tip of the radicle is formed on the lower end of the hypocotyl from the adjacent cell of the suspensor,

called the **hypophysis**. Thus, a complete embryo is formed consisting of the plumule, the radicle, the hypocotyl and two cotyledons. The suspensor is a temporary structure, which either remains for a short time at the tip of the radicle or soon disappears, and its place is ultimately occupied by the developing root. The progressively developed embryo, in this case, absorbs all the nutritive tissues, becomes curved and completely fills up the cavity of the embryo sac.

B. MONOCOTYLEDONOUS EMBRYO (Fig. 308)

The embryo of *Sagittaria variabilis* (Fam. Alismataceae)

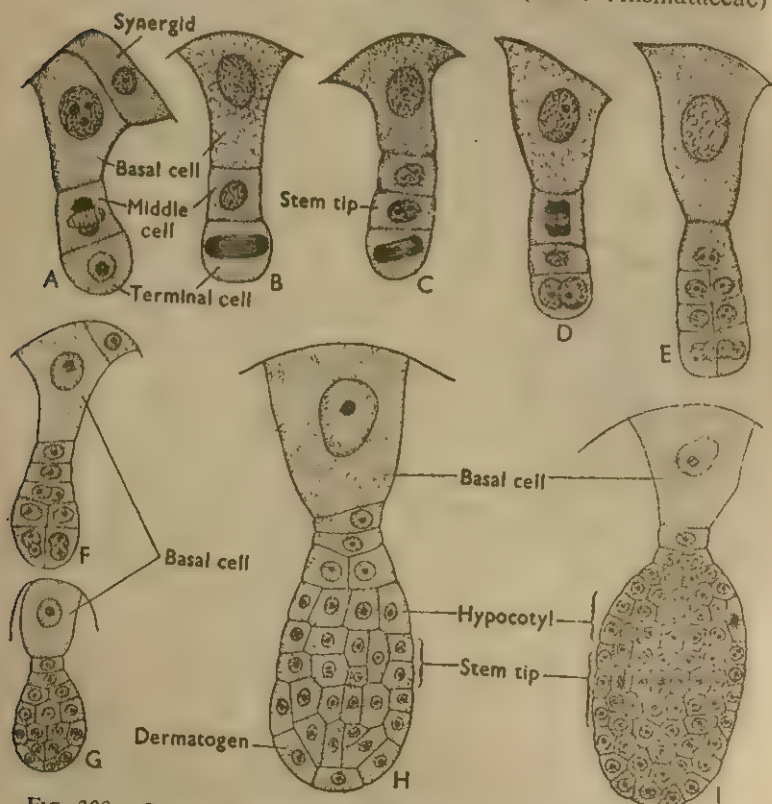


FIG. 308. GRADUAL STAGES IN THE DEVELOPMENT OF THE EMBRYO IN *Sagittaria variabilis*.

is usually taken as the representative type of the monocotyledonous embryo.

The **pro-embryo** of *Sagittaria* is a three-celled filament consisting of a **terminal cell**, a **middle cell**, and a large **basal cell**. The last one undergoes a considerable enlargement without any division, and forms the major part of the suspensor. The middle one undergoes a series of divisions, in both the transverse and vertical planes, and gives rise to the stem tip, the hypocotyl, the root tip, and the remaining portion of the suspensor. The terminal cell first divides by a vertical wall, and subsequently, walls are laid down in the two other planes. Thus, the **octants** are formed. The terminal cell gives rise to the **single cotyledon**. The stem tip arises laterally as a depression by the side of the embryo, so that the cotyledon becomes terminal in position.

It is, however, interesting to note that occasionally dicotyledonous embryos are developed in *Agapanthus* of Fam. Liliaceae. In this case, the tip of the somewhat massive pro-embryo broadens, and a cotyledonary zone with two growing points is produced at the margin. This zone then grows in an upward direction, ultimately forming a cotyledonary ring around the central depression, from which develops the stem tip. Either a dicotyledonous or a monocotyledonous embryo is finally produced, depending on whether both the growing points go on developing equally well, or only one continues to do so, while the other one is checked. Thus, it can be deduced from such a case, that though there may be a solitary cotyledon, which appears to be terminal, yet it is lateral in reality and the stem tip is terminal. Further, it points to the fact that the dicotyledonous condition is more primitive than the monocotyledonous one.

THE SUSPENSOR

By the term **suspensor** is generally meant the structure which is formed from the basal cell of the pro-embryo, or, in other words, the cell which lies nearest to the micropyle. In the embryos of caryophyllad type, it is usually made up of only one considerably enlarged cell. But, generally, the suspensor possesses a row or a mass of cells, which serve to attach the embryo to the micropylar end of the embryo sac. The function, however, may not be purely mechanical in nature, as in most members of Fam. Araceae, in many orchidaceous plants, as well as in a large number of genera belonging to different families, the suspensor is completely absent. In many cases, the suspensor cells greatly elongate, as is

commonly found in the gymnosperms. Such elongated suspensors take part in the conduction of nutrition to the embryo by pushing

the pro-embryo deep within the endosperm (e.g., *Trapa* of Fam. Onagraceae, *Dendrophthoe* of Fam. Loranthaceae, and others). They may also play a direct role in the nutrition of the embryo (e.g., members of the S.F. Papilionaceae, Fig. 309). The suspensor cells in such cases are rich in starch, and help in the absorption of food from the endosperm to supply the same to the developing embryo.

An interesting feature is the haustorial outgrowth from the suspensor cells, which has been found in many families like Caryophyllaceae, Cruciferae, Papaveraceae, Geraniaceae, Crassulaceae, Rubiaceae, Orchidaceae, etc. The simplest type of suspensorial haustorium is the highly elongated single suspensor cell itself of the

embryo of the caryophyllad type. In *Tropaeolum majus* (Fam. Tropaeolaceae), two haustoria arise from the base of the suspensor.

THE ENDOSPERM

Simultaneously with the development of the embryo, the endosperm nucleus undergoes successive divisions, resulting in the formation of many free nuclei within the enlarging embryo sac.

ter on, by the simultaneous formation of walls between these nuclei, a considerable amount of tissue is produced, which is known as the **endosperm**. The endosperm cells contain reserve foods, which are available to the growing embryo. The endosperm grows and fills up the major portion of the embryo sac,

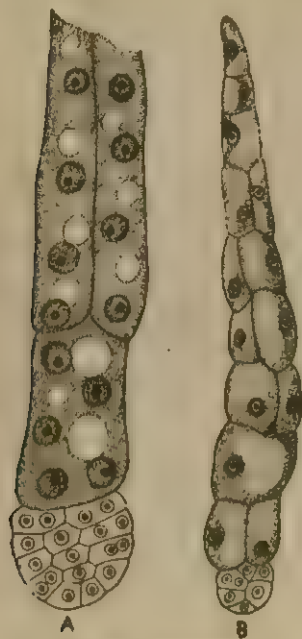


FIG. 309. SUSPENSORS
A, of *Pisum sativum*; B, of
Cicer arietinum.

excepting the space occupied by the developing embryo. In many plants, this tissue may encroach and destroy all the tissues of the nucellus. In a few cases, however, as in water lily (*Nymphaea lotus*) of Fam. Nymphaeaceae, cardamom (*Amomum aromaticum*) of Fam. Zingiberaceae, black pepper (*Piper nigrum*), cubeb (*Piper caninum*) and other plants of Fam. Piperaceae, etc., the nucellus persists and forms a considerable amount of nutritive tissue, called the **perisperm**, within the fertilized ovule. The developing embryo either consumes all the nutritive tissues (endosperm and perisperm), so that the entire cavity of the ovule with the integuments is completely occupied by it, or some portion of the nutritive tissue (either endosperm, or both endosperm and perisperm) is left unconsumed. When the nutritive tissue is entirely absent, the seed is **exalbuminous** or **non-endospermic**, as in pea, bean and other legumes, but when present, the seed is said to be **albuminous** or **endospermic**, as in castor (*Ricinus communis*) of Fam. Euphorbiaceae, custard apple (*Anona squamosa*) and other plants of Fam. Anonaceae, and all grasses (Fam. Gramineae), etc.

It is interesting to note that excepting the two families, Orchidaceae and Podostemaceae, endosperm formation takes place in all other families of angiosperms.*

In the majority of cases, the two polar nuclei first unite. Subsequent to this, a second union takes place between this fusion nucleus and a male gamete. But, a number of variations have been recorded in different families of angiosperms. For example, in the genera *Fritillaria*, *Gagea* and *Tulipa* of Fam. Liliaceae, *Zea* of Fam. Gramineae, and *Nicotiana* of Fam. Solanaceae, all the three nuclei unite simultaneously. In *Monotropa* of Fam. Pirolaceae, the micropylar polar nucleus and the male gamete first unite together, and then the antipodal polar nucleus comes and unites with it. In *Adoxa* of Fam. Caprifoliaceae, and in the Fam. Onagraceae, the endosperm nucleus is formed by the union between the micropylar polar nucleus and the male gamete only.

The division of the endosperm nucleus usually takes place prior to that of the oospore. As a result of this, the endosperm might have been considerably advanced in its development, even

* The endosperm in gymnosperms is normally a pre-fertilization product and a haploid tissue. It is considered there as the female gametophyte.

before the first division of the oospore has occurred. In extremely rare cases, however, the oospore may divide first.

There are chiefly *three* main types of endosperm development, namely the *nuclear type*, the *cellular type*, and the *helobial type*.

Nuclear type. In the nuclear type of endosperm development, the endosperm nucleus at first divides freely, the numerous nuclei lying scattered in the cytoplasm of the embryo sac, which rapidly begins to enlarge. Later on, wall formation takes place either progressively or synchronously throughout the embryo sac. In small-sized embryo sacs, however, this wall formation may start at a very early stage. In some cases, the nuclei remain free for an indefinite length of period, as in some members of Fam. Melastomaceae, S. F. Papilionaceae (Fam. Leguminosae), and others.

The embryo sac enlargement is associated with an enlargement of a central vacuole. As this vacuole enlarges, the cytoplasm is gradually reduced to a thin lining layer, in which the dividing nuclei lie approximately equidistant from one another. In some specialized cases, as in the genus *Hypericum* of Fam. Hypericaceae, a few of the nuclei at the antipodal end of the sac become separated from the rest by means of a membrane. Thus, a multinucleate cyst is formed, from which a haustorium is sent down into the chalaza. Swamy has termed it as the *Hypericum type of endosperm development*.

The cells, which are formed as a result of wall formation, at first contain a number of nuclei in each. If a single nucleus is included, it generally undergoes further divisions and gives rise to a multinucleate cell. Ultimately, however, all the nuclei fuse, and, excepting in rare cases, all the cells of the endosperm are uninucleate.

Cellular type. In the cellular type of endosperm development, the free nuclear divisions of the endosperm nucleus are unknown, because as soon as the first division occurs, the first wall formation takes place. The mode of cell formation is at first fairly regular, irregularities occurring later on. According to Schnarf, a few types may be differentiated based on the direction of the first cell walls, which may be longitudinally (e.g. *Adoxa* of Fam. Caprifoliaceae), transversely (e.g., *Verbascum* of Fam.

Verbenaceae, and members of Anonaceae and Ericaceae in general), or obliquely (e.g., *Myosotis* of Fam. Boraginaceae) placed in relation to the embryo sac, or the direction of the first wall may not be constant at all (e. g., *Gunnera* and *Senecio* of Fam. Compositae, and many members of Fam. Valerianaceae).

Helobial type. The helobial type of endosperm development is of rather restricted occurrence, and is chiefly found among members of the Order Helobiae. In this type, after the formation of the endosperm nucleus, a transverse wall is laid down, which divides the embryo sac into two portions. The antipodal portion is small, in which the nucleus either remains as such, without undergoing any further division, or it may divide just a few times giving rise to a maximum number of 64 nuclei. Formation of cell walls may also take place giving rise to a small mass of cells beneath the main body of the endosperm.

In the micropylar portion of the embryo sac, which is considerably large, the endosperm formation takes place as in the normal nuclear type. The antipodal mass of cells generally gets crushed and disorganized by the growth of this tissue.

A good deal of anomalies occur in the formation of endosperm, of which the **endospermal haustoria** or **caeca** need special mention. These may be of two categories, **micropylar** and **chalazal**, but frequently both may be found in the same ovule.

The micropylar haustoria may be unicellular outgrowths through the micropyle, and they ramify in a fungal mycelial fashion over the entire surface of the ovule and the ovarian wall, or penetrate the tissue of the funiculus and even the placenta. As the haustoria enlarge, free nuclear division takes place in them. The haustorium may be formed by an enlargement of the apex of the embryo sac (e.g., members of Fam. Labiatae), or by cell groups from the micropylar region of the cellular endosperm (e.g., *Vernonia* of Fam. Compositae and *Lobelia* of Fam. Campanulaceae). Such haustoria are commonly found in the families Bignoniaceae, Scrophulariaceae, Labiatae, some members of Lentibulariaceae, and others.

The chalazal haustoria are frequently formed from the antipodal cell, which is produced by laying down of the first transverse wall in the cellular type of endosperm formation. This cell may develop in an irregular pouch-like character, which

penetrates and finally destroys the tissue of the chalaza. The family Scrophulariaceae usually exhibits an interesting feature, as both micropylar and chalazal haustoria are produced at the two ends of the embryo sac respectively.

EMBRYO CULTURE

The seeds of many plants are often nonviable due to the arrested growth of the embryos, a fact which sometimes may cause economic loss even. This difficulty, however, may be overcome by excising the young embryos from the ovules and growing them on culture media. The fully-grown embryos are ultimately transplanted into the soil, as found in *Datura*, *Prunus*, maize, etc. Embryos may also be removed from some dormant seeds and successfully cultured on artificial media, as found in the *Iris* seed. This technique of growing partially developed embryos on sterile culture media is usually referred to as **embryo culture**.

Technique. The larger embryos can usually be dissected out with the aid of a needle by placing the seeds in between the fingers (Fig. 310), while a dissecting microscope is required for smaller embryos. The excised embryo is then placed in the

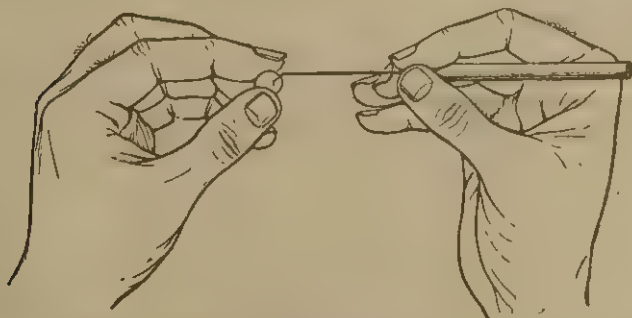


FIG. 310. FIGURE SHOWING THE REMOVAL OF THE EMBRYO FROM THE SEED.
(after Randolph).

artificial medium contained in the culture bottle (Fig. 311). As the conditions may facilitate the development of certain harmful micro-organisms (e.g., bacteria and fungi), aseptic measures should be taken; otherwise, contamination of culture results in the death of the embryo. The culture room

including the dissecting table should be sprayed with 1% solution of carbolic acid to avoid contamination by air-borne spores. The dissecting instruments should be dipped

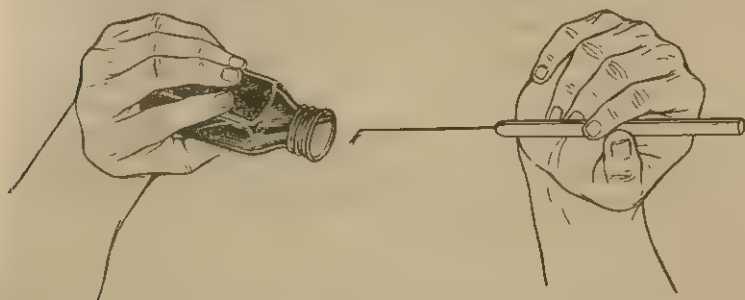


FIG. 311. FIGURE SHOWING THE INTRODUCTION OF THE EXCISED EMBRYO INTO THE CULTURE MEDIUM
(after Randolph).

in 70% alcohol and passed over the flame. The culture medium should be sterilized, and the excised embryo should be placed immediately into the sterile culture medium.

The embryo culture was first successfully done by Hannig (1904) who worked on certain crucifers, e.g., *Raphanus*, *Cochlearia*, etc., and used the culture medium containing sugars, mineral salts, plant decoctions, certain amino acids and gelatin. Stingl (1907) modified the method of Hannig, and grew embryos of certain cereals by transferring them to the endosperm of related genera. Dietrich (1924), however, demonstrated that Knops' solution with 2.5 to 5% sucrose and 1.5% agar was sufficient for the embryo culture. The development of young embryos may be stimulated, in many cases, with the addition of a small amount of coconut milk to the medium. The stimulation of embryo development is probably due to the presence of a growth-promoting substance in the coconut milk, This is termed as the **embryo factor**, which effects cell division. The mature embryos usually possess the embryo factor, as the ability of synthesis increases with age. Blakeslee and Satina (1944) are of opinion that malt extracts may possess the 'embryo factor' activity.

Importance. The embryo culture is of immense importance in several respects. To illustrate a few, the following *three* are worth mentioning :

1. The nutritive requirements of the developing embryos can be understood by this method.

2. *Iris* seeds require two to several years for germination. In such dormant seeds the time required to germinate can be shortened by adapting this method, which saves uncertainty and delay.

3. In some cases, it has been found that seeds produced as a result of distant crosses fail to attain maturity ; in such cases, viable embryos can be raised by means of embryo culture.

CHAPTER III

POLYEMBRYONY AND PARTHENOGENESIS

Polyembryony is the condition in which more than one embryos are formed within a seed. This is found in a large number of seed plants (both gymnosperms and angiosperms), in some of which it occurs very constantly. It may be produced in several ways. Sometimes, it results from the division of the oospore itself. In such cases, the basal cell of a two-celled proembryo undergoes repeated divisions forming the *embryogenic mass*, an irregular mass of cells. A few individuals may develop into embryos in addition to the normally developed one. Out of these embryos, one or two occasionally survive and reach maturity. Such a case of polyembryony can be found in plants like *Vincetoxicum nigrum* and *V. officinale* of Fam. Asclepiadaceae, *Limncharis emarginata* of Fam. Butomaceae, *Erythronium americanum* and *Tulipa gesneriana*, both of Fam. Liliaceae, and *Habenaria platyphylla* of Fam. Orchidaceae. In a few rare cases (e.g., *Linum usitatissimum* of Fam. Linaceae, *Empetrum nigrum* of Fam. Empetraceae, and some orchids), the very young embryo developing from the oospore splits up into two or three parts, each one developing into an embryo. This is known as **cleavage polyembryony**.

Accessory embryos may also develop from other cells of the embryo sac besides the one developed from the normal ovum. Frequently, one or more synergids may be converted into embryos. This may take place by fertilization with the help of another pollen tube carrying male gametes, or even without any fertilization, as in *Linum usitatissimum* (Fam. Linaceae) ; as a result, the twin embryos are a mixture of both haploid and diploid structures. In some species of *Lilium* and *Allium*, both of Fam. Liliaceae, *Iris* of Fam. Iridaceae, *Poa* of Fam. Gramineae, and others, such accessory embryos, formed from synergids, have also been recorded.

Occasionally, antipodal cells may also undergo fertilization and give rise to accessory embryos, as is found in *Elatostema* (Fam. Urticaceae), *Ulmus* (Fam. Ulmaceae), and *Allium odorum* (Fam.

Liliaceae). What happens ultimately to these embryos is as yet unknown.

In some cases, more than one embryo sacs may be developed within the same nucellus, but definite polyembryony from such a condition could not have been noted so far.

Any other type of embryo formation in which embryos arise outside the embryo sac, *i.e.*, adventitiously from the sporophytic tissue, is placed under an entirely different category. Such cases are recorded under the term **apomixis**. In its widest sense, this term includes all sexual methods of reproduction inclusive of the vegetative propagation.

Several other interesting phenomena occurring in connection with apomixis require some explanation. For instance, a diploid embryo sac may be formed directly from the megaspore mother-cell, and the diploid ovum produces the embryo without any act of fertilization. This is termed as **diplospory**, sometimes referred to as **somatic parthenogenesis** or **diplo-parthenogenesis**. In **true parthenogenesis**, however, a haploid ovum is formed, which develops into the embryo without any fertilization. In **apospory**, a diploid embryo sac develops from a somatic cell of the nucellus, and the formation of the embryo takes place as in diplospory. On the other hand, if a cell of a haploid or a diploid female gametophyte (embryo sac), excepting the ovum, gives rise to the embryo directly without any fertilization, it is called **apogamy** or **apogamity**.

Another type of embryo formation, termed as **adventitious embryony**, is a case of vegetative reproduction, which is closely related to vivipary (a special mode of germination, in which the embryo is produced vegetatively, either wholly or partly from the flower). In adventitious embryony, the embryos are directly produced from the diploid cells. Further development usually takes place within the embryo sac. **Pseudogamy** is another phenomenon, in which the stimulus of pollination is necessary for the formation of embryo, although actual fertilization is wanting.

It should be noted that the apomixitic genera are, as a rule, **polyploids***, *i.e.*, they exhibit higher chromosome numbers. They also behave in many respects like the hybrids.

* For a detailed discussion on **polyploidy**, refer to the section in Cytology.

CYTOLOGY

INTRODUCTORY CHAPTER

Cytology is that branch of biological science which deals with the structural as well as functional organization of a single or closely associated protoplasts with relation to metabolism, growth, differentiation and heredity. Although much work has been done in this branch during the present century, the foundation stone was actually laid down by the British naturalist Robert Hooke in 1665, when he first described the structure of the cork cells under the microscope. Robert Brown (1831) first pointed out the nucleus as a normal and characteristic component of every living cell. Following this, came the cell theory of Schleiden and Schwann (1839), which postulates that the body of every living organism is essentially composed of cells. According to them, the cells are thus 'the primary agents of organization'. In opposition to this, Sachs, de Bary, and others were of opinion that the entire multicellular organism, and not the cells, is to be regarded as 'the primary agent of organization'. According to these workers, therefore, the body of a multicellular organism was made up of a continuous mass of protoplasm, which was, in its turn, divided into several smaller compartments or centres of diverse activities,—the cells. Flemming (1882) described the process of mitosis and termed the stainable part of the nucleus as the *chromosomes*, which underwent longitudinal splittings during the process. Roux and Weismann (1884) observed that the individual portions of each chromosome were important in determining the morphology, physiology and development of an individual. Van Beneden and Hanser (1884) noted in this connection that during the process of somatic cell division the longitudinally halved chromosomes travel to the two newly-forming daughter cells. Van Beneden (1884) further observed that during fertilization equal numbers of chromosomes are contributed by the sperm and the egg in the formation of the zygote.

In addition to these, the name of Gregor Johann Mendel must be mentioned as the father and founder of the study of the present-day nuclear cytology.

CHAPTER I

FORMATION OF NEW CELLS

Plants, like animals, grow and multiply. When a plant is growing, there is a continuous formation of new cells in the growing parts. When there is reproduction, new cells are also formed. There can be neither growth nor reproduction without the formation of new cells. Cells that keep up the growth of the plant and carry on reproduction do not, however, arise as independent bodies, but are always formed from the mother cells. From these mother cells new cells are produced, and these daughter cells, in their turn, give rise to other new cells. This process goes on as long as the plant is alive and able to carry on its functions. The following are the common methods of new cell formation :

A. SOMATIC MITOSIS (Fig. 312)

The most common method of cell division is **somatic mitosis**, which takes place in the vegetative portions of the plant body. The cells constituting the vegetative parts of the plants are called **somatic cells**, and hence, the division of these cells is termed as **somatic cell division**. The phenomenon involved in the process of cell division is very complicated, where the nucleus of the cell undergoes division at first, thereby producing two indential daughter nuclei. The cytologists often term this cell division as **mitosis** or **karyokinesis**. The second division following the nuclear division is the cytoplasmic division, and is called **cytokinesis**.

Mitotic cell division may be described under *four* distinct stages with regard to the chromosome behaviour : (i) *prophase*, (ii) *metaphase*, (iii) *anaphase*, and (iv) *telophase*.

(I) PROPHASE

Before the onset of this stage, the nucleus of the cell does not undergo any visible change, and this condition is termed as the **metabolic condition** of the nucleus. The nucleus at this stage is commonly referred to as the **metabolic** or **resting nucleus**. The first visible change noticed in the

prophase is the appearance of the chromosomes as slender thread-like structures, called the **chromonemata**. The visibility of the chromonemata becomes increasingly clearer on account of their progressive dehydration. With the progress of prophase, the chromonemata tend to uncoil and become thick, as a result of which the double nature of the threads becomes apparent. These threads are, later on, called **chromosomes**. From the very beginning, the chromosomes manifest their doubleness, as well as longitudinally split condition. Each half of the chromosome is now referred to as the **chromatid**, which is regarded as the functional unit in the cell division.

The result of shortening and thickening of the chromosome is due to spiralization, which is intensely effected by the coiling phenomenon in the process. The coiling phenomenon was previously thought to be a very simple process, *i.e.*, on account of deposition of DNA over the chromosomes, and it was termed as **nucleination**. The modern cytologists opine that the amount of DNA is not the criterion to explain the observed changes in chromosomes. It has been suggested that the phenomena of condensation and other relevant changes noted in the chromosome during cell division take place due to the presence of DNA-histone-complex.

The end of prophase is marked by the gradual disappearance of the nucleolus and the nuclear membrane.

(II) METAPHASE

When metaphase follows, the demarcation between cytoplasm and nucleus disappears, and this stage is characterized by the appearance of a **bipolar spindle**, formed due to chemical changes in the **karyolymph** or **nuclear sap**. This spindle is also called an **achromatic figure**, because it has less affinity for the stains. The spindle structure is explained to be the result of certain molecular rearrangements in the material of cytoplasm. The two ends of the spindle are called the **poles**, and the middle region is the **equator**. The shorter and thicker chromosomes or chromatids remain aligned at the equatorial plane of the spindle. Each chromatid has a distinct region of attachment with the fibres of the spindle, and this point of attachment is termed as the **centromere** or **kinetochore**; it has further been referred to as the **primary constriction**.

The fibres, so attached directly to the bodies of the chromatids at the centromeric regions, are called **tractile fibres**. It has

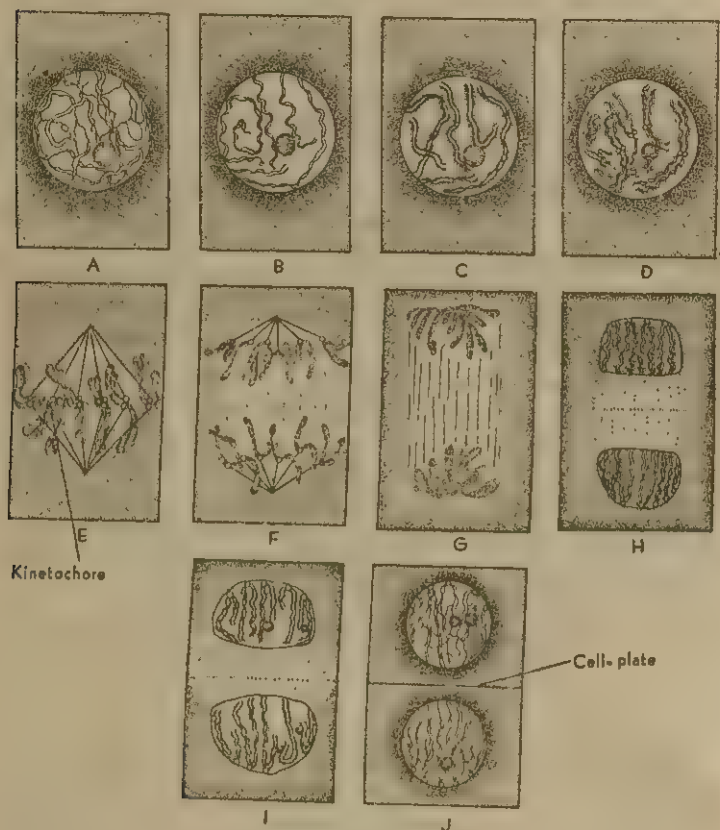


FIG. 312. STAGES IN MITOSIS
(Modified after Sharp).

recently been suggested that the tractile fibre is nothing but an extension of the chromatid or something secreted from the chromatid.

(III) ANAPHASE

At this stage, the chromatids become separate, and commence moving from the equatorial plane towards the two poles. In each set of these chromosomes (at each pole), there take place a

qualitative as well as a quantitative distribution of the original chromosome character. It is the centromere, divided in the late metaphase, which moves along the tractile fibre, keeping the arms of the chromatids behind. The usual configurations of the chromosomes at this stage are, as such, V- or L-shaped appearances, which depend on the relative lengths of the arms of the chromatids. The end of this stage is marked by the gradual disappearance of the tractile fibres and the matrix too.

The cause of the anaphasic movement is a debatable problem. This movement of chromosomes may be due to some attractive force exercised by the fibres, possibly on account of contraction of the constituent protein molecules of the fibres.

(IV) TELOPHASE

During this stage, the chromosomes complete their poleward movement, and reach the two poles. On reaching the poles, the chromosomes become clumped together, thereby losing their separate identity. The crooked chromonemata begin to associate closely, and start anastomosing to construct the new reticulum. The nuclear membrane and the nucleolus are reorganized.

Within the two newly reconstructed nuclei, complex changes take place, which, in brief, may be described as the reverse of the changes occurring during prophase, namely, the unwinding of the spirals, hydration and consequent unfixability.

The diploid nucleus, so derived in the telophase, possesses at least a pair of striking chromosomes, which have a constriction at one end, and nearby this point the matrix is not collected. The portion of the chromosome, which appears to be abstricted from the main body or remains apart beyond the constriction, is called the **satellite**, and such a pair of chromosomes are termed as **sat-chromosomes**. The constriction of the chromosome is referred to as the **nucleolus organizer**. The formation of nucleolus in the nucleus takes place due to the presence of the **sat-chromosomes**.

CYTOKINESIS

The cytoplasmic division initiates with the reorganization of the nucleus in the telophase. While the two nuclei are being

reconstructed, the equatorial region of the spindle widens, and along with the surrounding cytoplasm they constitute a faintly limited structure, the **phragmoplast**. It has the appearance of a ring in polar view, and is barrel-shaped in lateral view. Gradually, the fibrils extend outwards, touch the lateral walls, and finally disappear. Before the disappearance of this structure, a thin line of granules begins to form across the centre, and these ultimately unite to form the **cell plate**. It has been interpreted that the cell plate is partially contributed by the spindle and partially by the coalescence of the droplets deposited by the cytoplasm. Very soon, the cell plate undergoes physical and chemical changes, and is transformed into the inter-cellular substance, called the **middle lamella**. On the middle lamella new cellulose wall is again formed by the protoplast. The *primary walls* gradually become thickened forming *secondary walls* by further deposition of cellulose materials.

In some cases, cytokinesis may also take place by the furrowing of the cytoplasm.

B. MEIOSIS (Figs. 313-314)

Meiosis is a special kind of cell division, and it is the antithesis of fertilization, in the sense, that it halves the number of chromosomes. In most animals, meiosis occurs just prior to fertilization, and results in the formation of sexual cells, the *sperms* and *eggs*. Their union in fertilization results in the formation of a diploid zygote. In lower plants, such as algae and fungi, the haploid spores are produced as a result of fertilization followed by meiosis. Each of them germinates giving rise to a haploid thallus. This structure, the *gametophyte*, produces gametes by mitosis. The zygote, formed by the union of two gametes, undergoes reduction division without having any further growth. The higher plants have a much more complicated life cycle than animals, because two generations are necessary to complete the entire cycle. The resultant zygote becomes diploid, *i.e.*, it contains ' $2n$ ' number of chromosomes, the two sets being contributed by the two gametes, male and female. This ' $2n$ ' number is again reduced to ' n ' or haploid number after reduction division.

Meiosis consists of essentially two nuclear divisions, which follow each other in rapid sequence. Of these two divisions, the first division is popularly known as **reductional**, and the second one, **equational**. In earlier days, these two divisions were recognized as **heterotypic** and **homotypic** respectively. Now-a-days, they are termed as the **first meiotic** and the **second meiotic** divisions.

MEIOTIC DIVISION I

PROPHASE I

The present-day cytologists have found it convenient to subdivide the first meiotic prophase into the following *five* sub-stages :

(a) **Leptotene** or **leptonema stage**. In this stage, the chromosomes are found in diploid number, and they appear single throughout and not double. It is also interesting to note that the chromosomes become very long and thin threads, and possibly simulate with the chromonemata of the anaphasic chromosomes of the preceding mitotic division. Further, they assume more granular appearance than the chromosomes in prophase of a somatic mitosis.

(b) **Zygotene** or **zygonema stage**. The identical chromosomes begin to pair in the diploid cells. These chromosomes which form identical pairs are called **homologous chromosomes** or **homologues**. Each pair of homologous chromosomes is also termed as the **bivalent**. Darlington (1935) has opined that **synapsis** or **selective pairing** may start at any of the several places along the length of the chromosomes. It may be **proterminal**, **procentric**, or **intermediate**. At any event, the synapsis begins to proceed in a zipper-like fashion for bringing the homologous chromosomes together along their entire length.

(c) **Pachytene** or **pachynema stage**. The bivalents of the previous stage become more thick, and they continue gradually to become thickened. At the end of this stage, the centromeres of the chromosomes become more distinct, and each chromosome of the bivalent undergoes a longitudinal splitting forming two **chromatids**. As a result of splitting, the bivalents consist of two

pairs of chromatid strands, and hence, it is also called the **four strand stage**.

(d) **Diplotene or diplonema stage.** The initiation of separation of longitudinally split chromosomes of the bivalents takes place at the diplotene stage. The homologous chromosomes begin to move apart from each other as a result of loss in the pairing attraction with the formation of the chromatids. The paired chromosomes develop a tendency of holding together at

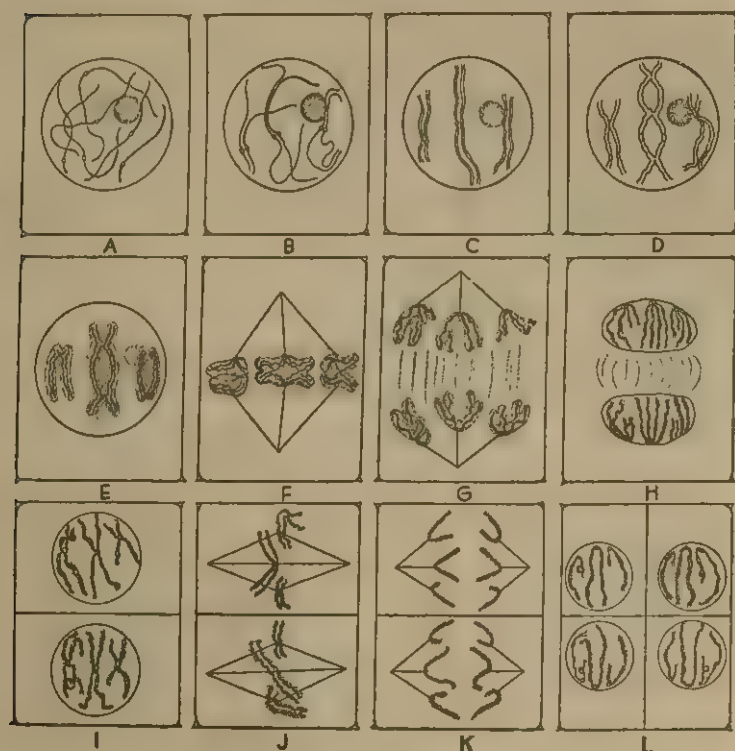


FIG. 313. STAGES IN MEIOSIS
(Redrawn from Sharp).

certain points along their length. Each point of contact is a **chiasma**, and it has been observed that two of the chromatids, one from each chromosome, cross over resulting in an X-shaped structure. It may be stated that the chiasma is a point of

exchange, which preserves the biavalent structure. The chiasmata, in some species, may be more frequent at the ends of the chromosomes, and they are, as such, called **terminal** in position. **Interstitial chiasmata** may be noted anywhere along the arms of the chromosomes. It has been presumed that terminal chiasmata may have their origin from interstitial ones, after which the chiasmata move towards the terminal position. This movement, which is responsible for shifting of chiasmata from one place to another, has been called **terminalization**.

(e) **Diakinesis**. The demarcation between the diakinesis and the diplotene stage does not appear to be a sharp one. The chromosomes in the diakinesis are found characteristically in a contracted state, and this stage is also characterized by the disappearance of the nucleolus from its associated chromosomes, as well as by the distribution of bivalents throughout the nucleus. On account of more tightly coiling, the shortening of chromosomes begin to continue. Consequently, the bivalents become more rounded in shape, and the homologues remain joined to each other at their terminal ends. This union of bivalents is effected due to terminalization of chiasmata, when the shortening of chromosomes commences.

METAPHASE I

The complete disappearance of the nuclear membrane and the formation of the spindle are the manifestations of this stage. The spindle (achromatic figure) is formed as usual in mitosis. The chromatids of tetrads begin to congress at the equatorial zone of the spindle.

ANAPHASE I

The chromosomes initiate poleward movements from the equatorial zone of the metaphase plate. The centromeres of each bivalent during the process remain undivided as they travel polewards, and as a result, the segregation of whole chromosomes (with two chromatids) instead of chromatids takes place. In this stage, each group of chromosomes consists of one set (haploid) of chromosomes in place of two sets (diploid) of chromatids. In this way, a reduction in chromosome number

takes place by the first meiotic division. The process of terminalization of the chiasmata is now over.

TELOPHASE I

The formation of a nuclear membrane and a regrouping of chromosomes occur next. The two newly formed daughter nuclei then undergo division II, after passing through a short **interphase stage** or **interkinesis**. The interkinetic stage is very variable, and the chromosomes (at this stage) become diffuse, and relaxation of their coiled structure takes place.

MEIOTIC DIVISION II

The commencement of the second division takes place practically as soon as the first one ends. The second division is termed 'equational'.

PROPHASE II

In this stage, the chromosomes are found to remain in association in *diads*, and the **matrix** begins to appear.

METAPHASE II

Here, the achromatic figure or bipolar spindle is again found, and the chromosomes align at the equatorial plane.

ANAPHASE II

The two chromatids of the diads move apart towards two poles along the fibres. The movement of centromeres takes place as usual, and the chromatids appear different in shapes.

TELOPHASE II

On reaching the poles, the chromatids reorganize into daughter nuclei, and thus four nuclei are formed. Each nucleus consists of a set of haploid chromosomes, and each set possesses one chromatid of each of the tetrads of Prophase I.

CYTOKINESIS takes place later on, giving rise to four cells, each with haploid or reduced number of chromosomes in the nucleus.

Cytokinesis in meiocytes or microsporocytes. The meiocytes (meiotic cells) or microsporocytes (microspore mother-cells)



FIG. 314. STAGES IN MEIOSIS
(Diagrammatic).

of the anthers in higher plants usually develop a cross wall at the close of the first meiotic division, and also in a plane at right angles to the axis of division. A second wall is laid down at right angles to the first, thereby dividing the cells at the end of the second meiotic division. In this way, four **microspores** or **pollen grains** are formed. They develop their characteristic walls and begin to enlarge, resulting ultimately in freeing themselves from the parent wall of the meiotic cell by dissolution. But, in certain angiosperms, such as, *Paeonia*, and some members of *Compositae*, the mode of wall formation differs to some extent from the former. In these latter cases, no wall formation takes place until after the second meiotic division. The two walls, at right angles to each other, begin to form simultaneously.

Differences between mitosis and meiosis***MITOSIS**

(i) Resting stage before mitotic division is prolonged.

(ii) Prophase is brief and substages are lacking.

(iii) Each chromosome splits longitudinally into two sister chromatids, and gradually becomes double within the common matrix, as the prophase advances.

(iv) There is no attraction between the split homologous chromosomes.

(v) Each chromosome with its centromere divides at metaphase, and the sister chromatids travel to either pole. So, the usual diploid number is restored.

(vi) Both sets of chromosomes, paternal and maternal, divide longitudinally and travel

MEIOSIS

(i) Resting stage before meiotic division is brief.

(ii) Prophase is long with distinct substages, such as leptotene, zygotene, pachytene, diplotene and diakinesis.

(iii) The chromosomes remain as single threads without any longitudinal splitting.

(iv) The homologous chromosomes show attraction towards each other at zygotene and the following stages in prophase of division I, and ultimately form bivalents. Due to chiasmata and crossing over, recombination takes place between paternal and maternal chromosomes.

(v) Each chromosome with its centromere does not divide, but the homologous chromosomes travel to either side. So, the diploid number ($2n$) is reduced to the haploid (n) one.

(vi) Only one set of chromosomes, either paternal and maternal, travels to either pole

* Modified after Sekharan and Sarathy (1960)

MITOSIS

to either pole. Thus, each daughter cell gets identical and equal number of chromosomes at the close of the mitotic division.

(vii) The separation of chromosomes at the early anaphase is caused by the repulsive force between the parts of the divided centromere.

(viii) There is only one nuclear division in mitosis. However, the daughter cells may undergo further divisions.

(ix) At the end of mitotic division, the chromosomes in the daughter cells do not differ qualitatively and numerically from those in the parent cells.

MEIOSIS

due to the orientation of the chromosomes at the equatorial region during the metaphase I.

(vii) The separation of chromosomes at the early anaphase is caused by the repulsive force between the centromeres of the homologues.

(viii) Meiosis consists of essentially two nuclear divisions, which follow each other in rapid sequence.

(ix) At the end of meiotic division, each daughter cell has haploid (n) and recombined chromosomes.

C. FREE CELL FORMATION (Fig. 315)

During this process, the nucleus divides by mitosis into two nuclei, each of which in its turn divides into two, and the process is repeated several times, until a large number of daughter nuclei are formed; all these lie free in the cytoplasm of the mother cell. Each daughter nucleus with its surrounding cytoplasm becomes separated from other nuclei by the progressive cleavage of the cytoplasm, so that many naked cells are formed within the original cell. These naked cells are ultimately discharged due to the rupture of the wall of the mother cell. In some cases, each of these naked cells, thus formed, rounds off and surrounds itself with a cell wall and lies free within the original cell. The wall of the mother cell bursts or disintegrates, and the cells are ultimately liberated. This type of cell formation is found in many algae and fungi. In gymnosperms, the development of the endosperm takes place by the process of free cell formation, but in a

slightly different way. After the formation of a large number of nuclei within the mother cell, formation of cell wall begins from the periphery, and this process proceeds towards the centre



FIG. 315. FREE CELL FORMATION
(Redrawn from Holman & Robbins).

forming a mass of united cells (tissue), called the **endosperm**. It is to be noted that by free cell formation the number of cells is greatly increased.

D. BUDDING OR GEMMATION (Fig. 316)

This type of cell formation is found among yeasts during vegetative reproduction. Yeast is unicellular! At the time of

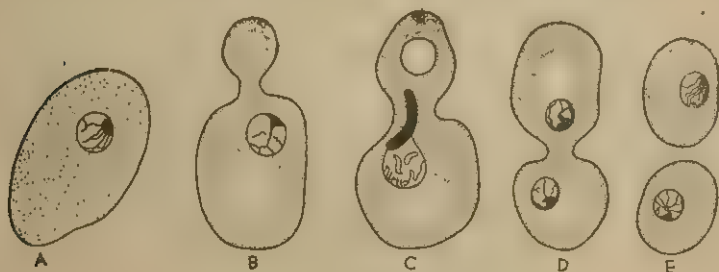


FIG. 316. STAGES IN THE BUDDING OF YEAST

budding or gemmation, a small protuberance or bud-like structure is formed on the cell wall, and it gradually increases in size.

Meanwhile, the nucleus divides into two daughter nuclei by mitosis, one of which, with some cytoplasm, enters into the gradually increasing bud. After the migration of one daughter nucleus, a wall is formed right across the constricted region, so that two cells are formed. By the ultimate splitting of this wall, the cells become independent of each other. This mode of cell formation is very rapid, so that within a very short time thousands of cells are produced.

E. & F. CONJUGATION AND FERTILIZATION •

These methods of cell formation occur during sexual reproduction. When sexual reproduction takes place, two naked protoplasts unite to form a single cell, known as the **zygote**, and the two uniting cells are known as **gametes** or sexual reproductive cells. In some cases, the gametes are distinctly differentiated into male and female ones. The male gamete is known as the **antherozoid** or **spermatozoid** or **sperm**, and the female one, the **ovum** or **oosphere** or **egg**. When union takes place between similar gametes, the process of union is known as **conjugation**. On the other hand, when the union is between male and female gametes, it is called **fertilization**. In both the cases, the product of union is a **zygote**. When the zygote is a product of conjugation, it is called the **zygospore**, and when it is the product of fertilization, the **oospore**. It is to be noted that in conjugation and fertilization, the number of cells is halved.

G. REJUVENESCENCE

By this process, the protoplast of the old cell becomes young and active again. When a cell becomes old, the protoplast recedes from the wall and aggregates at the centre of the cell. Afterwards, the cell wall bursts and the protoplast comes out, which moves freely in water for sometime with the help of flagella and then comes to rest, and finally secretes a new cell wall around it. This mode of cell formation is found in some algae, as in *Vaucheria*. In higher plants, young cells may be formed from the old ones without the production of flagella. It is to be noted that by rejuvenescence the number of cells remains constant.

H. PARTHENOGENESIS

During the sexual reproduction, a zygote (zygospore or oospore) is formed due to sexual union (conjugation or fertilization). In some cases, however, a special type of spore, known as the **parthenospore** or **azygospore** or **abospore**, is formed from one of the isogametes when conjugation fails, or from the female gamete only without being fertilized by the male one. This process of reproduction is known as **parthenogenesis**. It is found commonly in the lower plants, such as *Mucor*, *Spirogyra*, etc.

CHAPTER II

THE CHROMOSOMES

The components of a living plant cell have already been discussed in Part II. It has been stated there that the nucleus can never be formed *de novo*. It always originates by the division of the pre-existing nucleus, either directly (amitosis) or indirectly (mitosis). During the indirect division, the nuclear reticulum, at some stages, breaks up into definite number of bits or fragments. These are the **chromosomes**.

A cell **nucleus** is a protoplasmic structure bounded by a membrane. Its existence can be demonstrated in the absence of both cytoplasm and nuclear sap. It also includes the chromosomes, which can either be directly demonstrated or which were potentially demonstrable at a preceding cell division.

The study of the physical and chemical analyses of chromosome goes as far back as 1874. On chemical analyses, the presence of a protein component and another substance, known as nucleic acid, has been reported to be present in the nuclei. The nature of the chromosome had been an issue of considerable controversy. Recently, chromosome has been defined as a giant complex molecule made up of less complex chemical molecules, the **genes**, which represent the active regions in the chromosome thread.

By cytological observations it has been found that the nucleus has three different elements—the **chromatin**, the **nucleolus**, and the **nuclear sap**. The distribution of the chromatin threads in the nucleus shows typical aspects, according to the species and the kind of tissue. The phenomenon remains entirely obscure. The detailed study of the chromatin can give us information on structures close to the **genes**.

In 1781, Fontana described the nucleolar structure, which has an affinity for the eosine stain and is basophilic in nature. In 1931, Freitz pointed out that the nucleolus is associated with the secondary constriction region of the satellite chromosome of a given chromosome set. Matsuura suggested that as the different chromosomes contain the **nucleolus organizer**, competi-

tion exists for the formation of nuclei. Darlington and LaCour suggested that the nucleolus organizer can be located at any point on the chromosome, and not necessarily at the secondary constriction region. But, later workers like Gates, Bhaduri, and others proved that nucleoli are organized at the secondary constriction regions. Recent works with electron microscopy have revealed that the nucleolus contains two parts, one being essentially structureless (*i.e.*; amorphous), and the other being a fine, highly coiled, stranded material, the **nucleolonema**.

Serra considers that there are two methods of origin of the nucleolus : (1) they appear as droplets in the nucleoplasm and then coalesce to form the nucleolus ; (2) the nucleolar material is found throughout the entire length of the chromosomes, from the anaphase onwards, which accumulate at the secondary constriction regions, and later on contribute to nucleolus formation.

Chemically, the nucleolus is composed of ribose nucleic acid (RNA), the basic protein and the phospho-lipids. In addition to these, in some cases, deoxyribose nucleic acid (DNA) has also been reported. Of the enzymes, the most important is the alkaline phosphatase. The size of the nucleolus varies in different stages of the developmental cycle. In the cells, nucleoli not only serve as the reservoir of ribo-nucleic protein, but their roles in protein synthesis also has been demonstrated.

Bacterial nucleus. In many bacteria, the nucleus may be demonstrated by classical cytological methods. Works by Pickarshi, Rabinow *et al* reveal that a bacterial nucleus in very young cultures, consists of dumb-bell-shaped rods, lying transversely to the long axis of the bacterium, and dividing longitudinally. Bisset has shown that the nuclear structures are paired, and they divide even in young cultures, not by simple fission, but by some special method. Certain bacterial species do not possess this chromosome-like nucleus, but a vesicular structure is present in the resting cells. Similar types of nuclei are well known in Myxobacteria and sporulating bacilli. Despite superficial differences between the resting cells of various bacteria, the cytological processes accompanying their maturation are fundamentally similar. The chromosome-like vegetative nucleoids fuse to form a longitudinal rod-shaped fusion nucleus, which divides, and subsequently, recombines. The reduction

process in the sporulation of the large bacillus has been observed by Puluerttaft (1950) with the help of the phase-contrast microscope.

STRUCTURE OF THE CHROMOSOME

The structure of the chromosome (Figs. 317-318) can be best understood by a beginner with reference to the following points discussed below.

CHROMONEMATA. The chromosome is composed of a number of longitudinal subdivisions, called **chromonemata** (sing. **chromonema**), forming the gene-bearing portion and often showing doubleness; these are the **chromatids**. The chromatid is actually the functional unit in cell division. Furthermore, each chromonema is made up of several bid-like structures, termed **chromomeres**.

MATRIX. The chromonemata lie embedded within a **matrix**, which is achromatic in nature and is bounded externally by a **sheath**. Probably the function of the matrix is a protective one.

PRIMARY CONSTRICTION (CENTROMERE). Every chromosome is composed of two arms having a distinct or non-staining space between the two during the metaphase stage. This gap or space is known as the **primary constriction region**, in which the **centromere** is located. According to the position of the centromere, the chromosome may be (a) **metacentric** (median position), when constricted at the middle, or (b) **acrocentric** (submedian position), when constricted near about the top. Besides these, intermediate types also exist. The centromere is responsible for the movement of chromosomes to different poles, hence it is a specialized region of the chromosome. Formerly, it was supposed that the centromere is composed of compound genes, of a fluid substance, of a chromatic

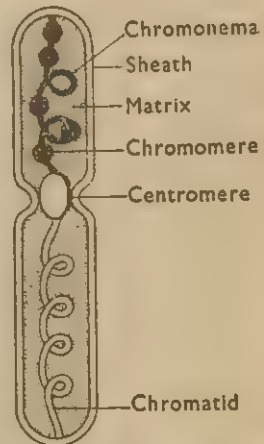


FIG. 317. MORPHOLOGY OF ANAPHASE CHROMOSOME (Modified after Swanson).

core an an achromatic covering, or of different lamellae. The centromeres are responsible for the shapes of chromosomes as they move poleward, and are partially responsible for the formation of the chromosomal fibres in the spindle. In exceptional cases, it relinquishes its role to secondary centres of movement. Normally, a centromere does not occupy a terminal position. Structurally, the centromere may be a non-staining constriction with no morphological evidence of structure, or may be a distinct body, also non-stainable and structureless, and somewhat longer in diameter than the remainder of the chromosome (as in maize) ; it may also be a tiny stainable granule, connected by thinly stretched threads (as in *Tradescantia*). The distinct demonstration of the quadruple chromosome structure of centromere, worked out by Tijo and Levan, has helped to clarify the structure. Darling (1940) has suggested its compound gene nature. In majority of higher plants, some special types of centromere have been found. **Dicentric** chromosomes have been found to contain two centromeres (as in some species of wheat). The **polycentric** chromosome has been found in *Ascaris megalocephala*, a kind of round worm. Recently, Camara *et al* have demonstrated the existence of diffused centromere in *Luzula purpurea*.

In certain algae (Myxophyceae), no distinct nucleus has been found, the corresponding structure being the "central body". It does not contain any chromosome but possesses genic matters, *i.e.*, DNA and protein. This may represent an early step in evolution, where gene particles are diffuse throughout the cytoplasmic mass, and there is no localization of function. The presence of diffuse centromere in some Conjugales as well as in primitive higher plants suggest that in the latter, the centromeric function has not been localized, although genes are arranged on discrete bodies—the chromosomes, their arrangement being linear.

A still higher step in chromosomal evolution is represented by plants possessing not only localized centromeres, but also a large number of secondary constrictions or unstained gaps in the chromosomes of *Fritillaria*, *Triticum*, etc. All these constrictions are, in some cases, concerned with the nucleolar organization.

The culmination of the series, *i.e.*, the final step, is represented by the majority of higher plants, where centromeres are present

for centromeric functions, one secondary constriction for nucleolar function, and one heterochromatic region for heterochromatic function, in chromosomes.

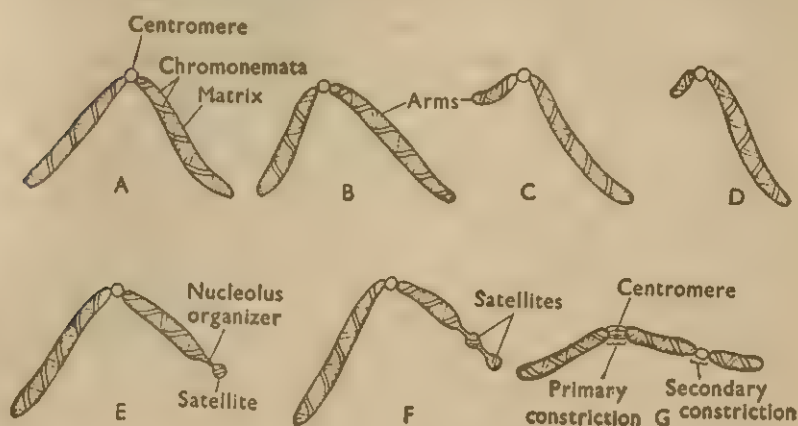


FIG. 318. CHROMOSOMES

A, metacentric; B—D, acrocentric; E—F, sat-chromosomes; G, a single chromosome with both primary and secondary constrictions.

SECONDARY CONSTRICTION. In addition to the primary constriction regions, some of the chromosomes possess a **secondary constriction region**, responsible for the organization of the nucleolus. If the secondary constriction is located at the end of the chromosome, and the distal segment is very small, the term **satellite** is applied. Some authors like McClintock claim the presence of a structure located at the base of the satellite stalk, known as the **nucleolus organizer**. The secondary constrictions may be induced by low temperature, as in *Trillium*.

TELOMERE. Müller (1938) termed the terminal end structure of chromosome as the **telomere**. The intact end of a chromosome does not enter into permanent association with other parts of the chromosome, and the loss of the telomere imparts an instability to the chromosome. In *Secale*, the telomeres seem to be able to look over the function of centromeres. Telomeres do not unite permanently with other telomeres, or with any other parts of the chromosome.

EUCHROMATIN AND HETEROCHROMATIN. Chromosomes are made up of two kinds of chromatin,—**euchromatin** and **heterochromatin**. Euchromatin contains the gene types, and heterochromatin is generally devoid of genes. Chemically, heterochromatin is more or less continuously and heavily “coated” with nucleic acid, and euchromatin varies in nucleic acid coating from cell to cell. Basically, these two types differ in coiling reaction.

CHAPTER III

VARIATIONS IN CHROMOSOME STRUCTURE AND NUMBER

I. STRUCTURAL CHANGES IN CHROMOSOMES

Various structural changes leading to chromosomal aberrations have been met with in plants. A very brief account of the same is given below.

A. CHANGE IN NUMBER OF GENES

(1) **DELETION AND DEFICIENCY** (Fig. 319). A **deficiency** involves the detachment and loss of a portion of an arm from the remainder of the chromosome. The deleted portion will not survive if it lacks a centromere, since it will have no power in anaphasic movements. The deficiencies are either *terminal* or *interstitial*. An interstitial deficiency may also be termed as **deletion**.

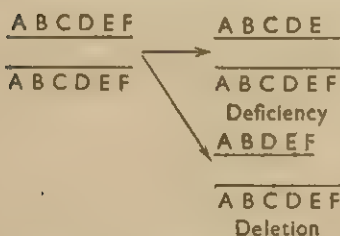


FIG. 319. DEFICIENCY AND
DELETION OF GENES.

ABCDE represents deficiency, and ABDEF represents deletion. The loss of gene (or genes) is not lethal in a heterozygous condition, while it becomes so in a homozygous one.

(2) **DUPLICATION** (Fig. 320). The presence of an extra piece of a chromosome, whether attached by some manner to one of the members of the regular complement, or existing as a fragment chromosome, is known as **duplication**. Here ABCDEFF represents duplication, and the gene F is repeated.

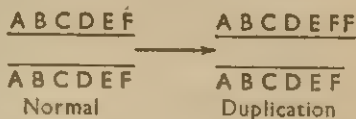


FIG. 320. DUPLICATION OF GENES

B. CHANGE IN ARRANGEMENT OF GENES

(3) **INVERSION** (Figs. 321-323). An inverted chromosome is one, in which a portion of the gene sequence has been rearranged in a reverse order. If confined to a single area of the chromosome, such a rearrangement is a **paracentric inversion**; if it includes a centromere, a **pericentric inversion** results.

The inversion of the segment BC in a normal chromosome ABCDEF leads to change the sequence of genes as ADCBEF (Fig. 320). In a heterozygous condition, the inverted portion forms a loop (Fig. 322) to get the corresponding alleles. The inversion in

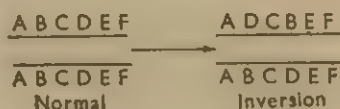


FIG. 321. INVERSION OF GENES

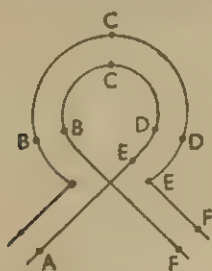


FIG. 322. LOOP DUE TO INVERSION.



FIG. 323. INVERSION BRIDGE IN ANAPHASE.

dicentric chromosomes is often characterized by the chromatin bridge (Fig. 323) at anaphase I during meiosis.

(4) **TRANSLOCATION** (Figs. 324-325). Fragmentation of two chromosomes and the mutual exchange through reunion of the fragments is known as **reciprocal translocation**. A **simple translocation** involves the transfer of the end of one chromosome to the end of another, occurring rarely. A **shift** is a translocation, in which one interstitial piece is removed from the arm of one chromosome, and is either re-inserted into the same arm but at a different location, or is shifted to an interstitial position on the other arm, or on a non-homologous chromosome.

Simple translocation : ABCF and UVWXYDEZ.

Reciprocal translocation : ABCXYZ and UVWDEF.

In heterozygous condition, the translocated chromosomes form a cross-like configuration. (Fig. 325).

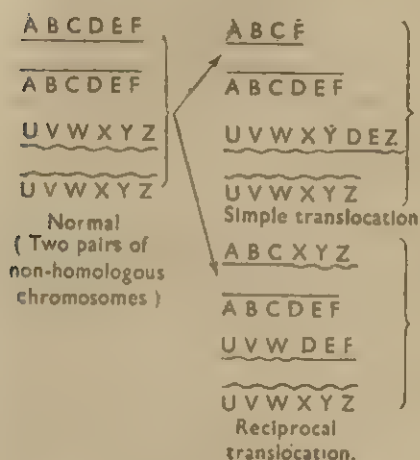


FIG. 324. TRANSLOCATION OF GENES

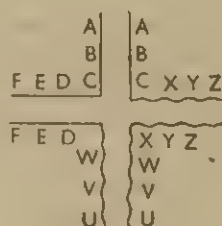


FIG. 325. TRANSLOCATION OF GENES.

Due to translocations, chromosomes may form ring or chain involving infinite patterns and leading to the **translocation complex** (as in *Rheo discolor*).

Translocations and inversions are the most common chromosomal aberrations. They are noticed in a number of species with very little effect on external morphological and physiological adaptive features.

The chromosomal aberrations may be *spontaneous* or *induced*. **Spontaneous aberrations** are stimulated by the deficiencies of calcium and magnesium in the medium in which the plants are grown. **Induced aberrations** are produced by various chemicals. For example, *colchicine* produces a general blockage of mitotic division or a destruction of the spindle.

The chromosomal aberrations have some evolutionary significance. "Structural changes bring about new genic interactions within the genotype, and consequently, the interaction with the

environment also changes"*). Thus, it is an important footing to evolution.

II. POLYPLOIDY

In normal cases, the somatic or body cells of plants exhibit twice the number of chromosomes as are found in the reproductive cells or gametes; the former are known as **diploids**, and the latter, **haploids**. This doubling in number of chromosomes takes place as a result of fertilization, i.e., the union between two haploid gametes, one of which is the male and the other, the female.

It has already been pointed out that the chromosomes are the carriers of **genes**, which are normally stable bodies, but may occasionally undergo changes or mutations. Changes in the chromosomes, thus, bring about corresponding changes in the general compositions of the organisms. As a result of changes in the chromosomes, an increase in their number in some multiples of the haploid number commonly takes place. This phenomenon is termed as **polyploidy**. Thus, normally, if the haploid number of chromosomes be designated by ' n ', the diploid number will be ' $2n$ ', the triploid ' $3n$ ', the tetraploid ' $4n$ ', and so on.

The first authentic report on polyploidy was based on the observations of De Vries in *Oenothera lamarckiana* (Fam. Onagraceae) grown under controlled conditions. The polyploid plants or **polyploids**, in this case, were rather more robust than the normal ones and had larger cells and larger nuclei, containing 28 chromosomes instead of 14, the normal diploid chromosome number. Since then a large number of cases of polyploidy have been reported from time to time in experimental materials investigated by different workers. Of these, plants like *Primula kewensis* (Fam. Primulaceae), *Raphanus brassica* (Fam. Cruciferae), etc., deserve mention.

CLASSIFICATION OF POLYPLOIDY

A. MULTIPLICATION OF ENTIRE SETS : EUPLOIDY

(1) **Autopolyploidy**. When the total gene content of the chromosomes (*genome*) of a particular species undergoes multi-

* Sekharan & Sarathy, 1960.

plication, it is called **autopolyploidy**. e.g., triploidy ($3n$), tetraploidy ($4n$), pentaploidy ($5n$), hexaploidy ($6n$), etc., against the diploidy ($2n$) of the normal plant.

Sometimes, the haploids (n) are also referred to this group.

(2) **Allopolyploidy**. The multiplication of the genome due to the result of crossing with another species, is termed as **allopolyploidy**. The allotetraploid, usually known as the **amphidiploid** of *Raphano-brassica* is the common example.

B INCREASE OR DECREASE IN THE NUMBER OF CHROMOSOMES IN A DIPLOID : ANEUPLOIDY OR HETEROPLOIDY OR IRREGULAR POLYPLOIDY

Due to irregularities in cell division, one or more chromosomes are either added to or subtracted from the original diploid number, resulting in chromosome numbers like ($2n+1$), ($2n-2$), ($2n-1$), and so on. The supernumerary chromosomes may also be responsible in bringing about changes as noted in maize, moss, etc. If these changes are of sufficient magnitude, and are transmissible from one generation to another, new species originate from the mutants.

(1) **Monosomics** occur in diploids, where one chromosome is lost ($2n-1$), e.g., *Datura*, *Nicotiana tabacum*, and *Triticum aestivum* (= *T. vulgare*), etc.

(2) **Polysomics** occur in diploids, where one or more chromosomes are added : **trisomics** ($2n+1$), **tetrasomics** ($2n+2$), etc.

The tetrasomics ($2n+2$) are found in wheat (*Triticum aestivum* = *T. vulgare*) of Fam. Gramineae. Trisomics ($2n+1$) are usually differentiated into **secondary trisomics** and **tertiary trisomics**. In some cases, **double trisomics** ($2n+1+1$) are also noted. Trisomics are found in various plants (belonging to widely different families of angiosperms), like *Datura*, *Lycopersicum*, *Nicotiana*, *Triticum*, *Zea*, etc.

(3) **Nullisomics** represent the loss of one pair of chromosomes in a diploid ($2n-2$). Serra noted normally growing plants of *Triticum aestivum*, which were nullisomics.

Polyploid forms usually appear as a result of irregularities taking place during mitosis or meiosis. In mitosis, sometimes the cell wall is not formed after the nuclear division ; or during

the anaphase stage, the sister chromatids fail to get separated for their poleward journey, consequently, leading to the doubling in chromosome numbers. Similarly, during meiosis, there may be failures in divisions, either in the first, or in the second, or in both. Sometimes, the homotypic spindles fuse, while in others, double division of chromosomes may take place during both the reductional as well as equational divisions of a meiotic process. As a result of all such aberrations, polyploid gametes are produced.

Polyploid shoots have been found to arise in a number of cases, where these are developed from buds produced from the callus tissues, which have been generated for the purpose of rapidly healing up the wounded or injured portion of a plant.

As the polyploids are important both economically as well as from the breeders' standpoint of view, these are artificially raised by several methods. Of these, the more commonly employed ones are as follows :

(a) Callus tissues are artificially produced by causing injuries to the plant, and vegetative buds are induced to be formed from such tissues.

(b) When the zygote is going to divide for the first time, the flower is alternately subjected to heat and cold shocks.

(c) The vegetative and flowering buds are treated with different kinds of rays of light.

(d) Different types of chemicals, like colchicine, gammexane, acenaphthene, *etc.*, are generally applied to both vegetative as well as reproductive buds.

In India, effective treatment with colchicine has raised polyploids in some plants like gram, chilli, cotton, jute, tobacco, and some cereals. The effective action of this chemical on a plant is usually indicated by the following symptoms :

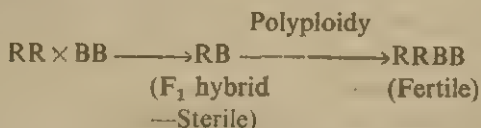
(i) The growth of the plant is immediately arrested.

(ii) The leaves and flowers grow larger in size, and if hairs are present on them, they also become coarser ; the stomata increase in size.

(iii) The formation of flowers takes place at a later period.

SOME IMPOTANT POLYPOIDS

1 *Raphano-brassica*. This is an example of an amphidiploid. The hybrid arising as a result of an intergeneric cross between *Raphanus sativus* and *Brassica oleracea* shows irregularities in pairing during meiosis, and becomes sterile, as the nine haploid chromosomes of each are distinctly different from the other. But with the introduction of polyploidy, it again becomes perfect and fertile.



(Let R and B represent genomes of *Raphanus* and *Brassica* respectively).

2. *Trisomics of Datura*. A series of twelve trisomics has been reported in *Datura stramonium* by Blakeslee and co-workers. This plant has $2n=24$, and twelve different trisomics have arisen as expected, each with a distinguished appearance.

3. *Common rice as the secondary polyploid*. The meiotic behaviour of common rice (*Oryza sativa*) having $2n=24$, suggests that it has arisen from some unknown ancestor (*Zizania sp.*) with $n=5$. It is more probable that one of the chromosomes of *Zizania sp.*, due to meiotic irregularity, gives rise to a stock having $2n=12$. This stock by the duplication of the genome gives rise to the common rice (*Oryza sativa*) having $2n=24$.

SIGNIFICANCE OF POLYPOIDY

The study of polyploids is of great significance to the plant breeders, as it has played a very important role in raising new types of economic plants. As polyploidy brings about quantitative changes in the genomes, it offers a very wide scope in affecting favourably the desirable characters in a particular species. Further, a knowledge of this phenomenon helps in understanding the relationships of different species, and thus aids in planning the hybridization experiments for rearing up improved types of crops.

CHAPTER IV

THE GENES

The gene is the structure for the determination of heredity. To define gene, it can be stated that the concept of gene is a logical expression of the hereditary character it determines. There are several ideas put forward to explain the concept of gene. The first one of the series is "it is the ultimate unit of recombination", *i.e.*, genes are those parts of chromosomes, between which crossing over might take place.* The genes are thus having a linear arrangement. The gene is also defined as the "ultimate unit of mutation." A third definition of gene states that "it is a unit of physiological activities." The fourth definition of this series is relating that "a gene is the ultimate unit of self-reproduction" (Pontecarvo, 1952). In whatever way the genes might be defined, it is a fact that they are very specific in their nature.

Mendel supposed that there was one factor for each of the phenotypic characters expressed in the offspring and each allelomorph was a distinct unity.

Bateson and Punnett supposed that an organism, which exhibited a dominant character, possessed a factor which was absent in an organism showing recessive characters. Later, of course, it was found that more than one factors could be allelomorphic to a dominant factor.

Johansen and Morgan stated that the theory of presence and absence was upset by the occurrence of more than two allelomorphs at one locus. The presence and absence theory thus assumes quantitative difference between the dominant and recessive allelomorphs. It seems necessary to assume that there is also a quantitative difference between the dominant and recessive factors.

Certain crossing over and radiation studies have limited the maximum size of a gene. It is supposed that the maximum length in this case is tens or even hundreds of the Angstrom unit.

A gene is an extremely dynamic but stable structure, and remains unchanged through generations. Its stability can be influenced by various chemical actions and also by radiation.

GENE MUTATIONS AND CHROMOSOMAL ABERRATIONS. Gene mutations are rearrangements of chromatin, with breakage being invariably involved (Goldschmidt, 1946, '51). Most geneticists, however, consider that the 'point mutation' is an intramolecular change in the gene without rearrangement of chromatin. The strongest evidence supporting point mutation is their reversibility.

Chromosomal aberrations are usually induced artificially by radiation with X-rays, gamma rays or ultra-violet rays, variation in temperature or by different chemical treatments, *etc.*

Chromosomes are now considered as complex giant molecules of several less complex chemical molecules, and the genes are the active sites of the chromosome thread forming the biological unit of control for heredity. The structure of a chromosome is said to have a nucleic acid core with a surrounding mass of protein. Opinions differ as to which of the components, *i.e.*, nucleic acid or protein, is responsible for the specificity of genes. At the same time some authors are suggesting the entire nucleoprotein compound to be responsible for the gene specificity. In connection with this, reference may be made to the different theories that have been proposed from time to time.

(1) **Protein theory** (Frey-Wyssling, *et al*). Proteins with diverse combination of different amino acids forming the polypeptide chain can satisfy the diversity of genes.

Even recently, this theory has been accepted by the majority of the investigators. But the recent discovery of the pneumococcal transformation by Avery has conclusively proved the nucleic acid concept.

(2) **Nucleic acid theory** (Matzia, Mirsky, and others). Some of the authors consider that only the nucleic acid alone is responsible for the gene specificity. But there are two objections raised against this theory :—(a) the variety of chemical morphology required for the control of different genetic trait is not present in the nucleic acid ; and (b) the transitory appearance of the nucleic acid also cannot support its gene nature.

(3) **Nucleo-protein theory.** According to Schultz, nucleoprotein as a whole is the gene, and he draws attention to their property of autocatalytic reproduction and specificity. He also states that as protein and nucleic acid both can satisfy the genetic requirements, the compound as a whole should be considered as a gene.

CHARACTERS OF GENES

Autocatalysis. Every gene can produce its own kind.

Heterocatalysis. During autocatalysis of genes, certain by-products are thrown off; these by-products combining with the cytoplasm help in the formation of enzymes. Hence, autocatalysis and heterocatalysis are corollary phenomena.

Mutation. A gene may undergo sudden changes, and this phenomenon is called **mutation**. Changes may be as regards its constitution or position (**position effect**), or regarding its complete or partial obliteration (**deletion**). All these changes may result in the expression of a changed phenotype.

SEX-LINKED GENES. Certain characters of some genes are often associated with the expression of a particular sex. The commonest sex-linked human trait is red-green colour-blindness. Its peculiar mode of transmission shows that it is a sex-linked recessive carried in the 'X'-chromosome. Due to the presence of two 'X'-chromosomes in their chromosome set, females are not colour-blind, unless in some rare cases. But 'X'-chromosomes are carriers and transmit the condition in 50% of the male population.

GENE ACTION. The problem of gene action has been carried out in detail by Beadle and Tatum in the fungus *Neurospora*. Strains of this fungus have been studied, each of which differs from the normal wild type by a single mutant gene. One of these mutants fails to grow in a medium deficient in the vitamin thiamine, another requires pyridoxine, still others require nicotinic acid, and amino acids, like arginine, lysine, valine, etc. It has been supposed that during the synthesis of those particularly required substances, one of the steps are changed, and so a mutant species cannot synthesize that substance within its body. Further, the particular organism will not grow unless that substance is

supplied to it. It has been shown that the absence of a certain enzyme, responsible for certain steps, is correspondingly associated with a single-gene difference. In human beings different diseases are on record where single-gene difference becomes the causative factor. Persons suffering from alcaptonuria always excrete black urine, because in them the homogentisic acid is not converted into urea, due to the absence of the controlling enzyme. Thus, Beadle considers that the relationship between the gene and the enzyme is 1 : 1.

The similarity between gene and enzyme is specially considered due to the fact that both are proteins having a capacity of autocatalysis.

Meischer in 1874 first studied the chemical nature of chromosomes. He first isolated a protein component and a substance, called *nuclein*, from the animal cell nuclei. Then different investigators like Kossel and others similarly worked out, and the final conclusion as regards the chemistry of chromosome is that it is a continuous framework of protein of the histone type, on which deposition of nucleic acid materials takes place during certain phases of cell division. In 1924, Feulgen and Russenbeck discovered "Feulgen reaction" and proved the presence of DNA (deoxyribose nucleic acid) in chromosomes. Several other methods have been applied for the same purpose, and in all cases DNA is found to be present in the chromosomes.

In recent years, Mirsky and Ris have isolated the chromosomes from the tissue and have made a direct chemical assay of the same. The extracted chromosome after chemical analysis has yielded the presence of both DNA and RNA as well as basic and non-basic proteins.

Deoxyribose nucleic acid (DNA). DNA is a giant molecule, several million times as heavy as an atom of hydrogen. Chemically, a molecule of DNA is made up of hydrogen, oxygen, nitrogen, carbon and phosphorus in the form of two long chains. These chains are made up of 2 alternate sugar and phosphate groups. It is found in the chromosome of the nucleus. During the division of nucleus, the amount of DNA present in it becomes double; so, when two nuclei are formed, each gets half of the increased amount of DNA, and thus the amount of DNA remains the same in all the nuclei. In higher organisms, DNA itself is

combined with protein. But according to the present-day theory, the protein is not involved in the production of DNA.

The deoxyribose nucleic acid has two main functions : the first function is to transmit all the hereditary information from the parents to the offspring, and the second one is to direct the formation of proteins.

The usual complicated nature of the DNA molecule contains eight different kinds of groups of atoms. The geometric picture of DNA has been worked out by the process of X-ray defraction, crystallography, etc.

Chemically, DNA is made up of units, known as **nucleotides**. Each nucleotide is a combination of phosphoric acid (H_3PO_4), a sugar called "deoxyribose" and a "purine" base (adenine or guanine) or a pyrimidine base (thymine or cytosine). They are connected as follows :

- (1) Phosphoric acid—deoxyribose—adenine.
- (2) Phosphoric acid—deoxyribose—thymine.
- (3) Phosphoric acid—deoxyribose—cytosine.
- (4) Phosphoric acid—deoxyribose—guanine.

In a single DNA molecule, there may be (as shown above) several thousand nucleotides, each being connected with the other by means of phosphoric acid. So DNA is a "polynucleotide".

The DNA code (*i.e.*, the sequence of adenine, thymine, etc. base) maintains the constant nature of every cell of each individual of all species of plants and animals. But there are certain ways, by which this stubborn nature of heredity is altered. These slow alternations of over millions of years could account for the development of the many varied forms of life.

When a sperm joins the egg, the DNA from each parent forms the code for a new life. In both sperm and egg half the amount of DNA is present. So, when these two unite, the amount of DNA present in the mother cells will be restored.

It has been very carefully noted that the sperms or eggs coming even from the same individual are not identical. That is what makes the difference between the children of the same parents, of course with the exception of identical twins. So, it is assumed that the DNA in each individual is unique to itself.

MUTATION AND DNA. DNA is now-a-days held responsible for all sorts of mutations in the living cell. What actually happens during mutation is not clearly known, but it has been guessed that probably a whole piece of molecule is left out or inverted or transposed when the DNA coil is open.

Mutations have been induced by ultra-violet light, ultrasonic agitation, chemicals, changes in nutrition, and even by virus infections. It has also been noted that once the cell nucleus is changed by the mutation of a gene, that change is persisting.

Ribose nucleic acid (RNA). The DNA information is transferred through another nucleic acid, called RNA, which has got almost the same structure as DNA, the only difference being in the nature of the sugar present. DNA contains deoxyribose sugar, whereas RNA contains ribose sugar. RNA is present in the cytoplasm and the nucleolus, whereas DNA is present only in chromosomes. RNA somehow picks up the hereditary information from the molecule of DNA. It then migrates out from the nucleus into the cytoplasm of the cell. In cytoplasm (in aggregates, called **ribosomes**), it directs the formation of proteins. The messenger RNA is supposed to determine the kind of protein synthesized by the ribosome.

RELATIONSHIP BETWEEN CYTOPLASMIC PROTEIN, DNA AND RNA

The relationship between DNA and cytoplasmic protein synthesis has been worked out by different authors in various ways. The controversial issue mainly involves the origin of RNA molecules from DNA. A good amount of controversy also exists about the synthesis of cytoplasmic proteins. Proteins are the important constituents of enzymes. As the gene action is controlled by enzymes, the synthesis of protein must also be a gene-controlled action.

A fact has been noted that RNA content is always associated with heavy-protein synthesis. The role of "**transfer or carrier RNAs**", which are mononucleotides as compared to the "**ribosomal or messenger RNAs**", which are polynucleotides—is different. It is now clear that the "carrier RNA" attaches itself to a specific amino acid in the cytoplasm, and finally brings it to the surface of the "ribosomal RNA". The action of

several "carrier RNAs" jointly contribute to the seat of formation of several amino acids, from which ultimately by the process of condensation, polypeptide proteins are produced. Recently, from the nucleolus three types of RNA have been isolated. It is assumed that these RNAs are actually directly derived from the DNA coil, and after slight modifications they change into "messenger RNAs"; the "carrier RNAs" are possibly formed from the "messenger RNAs". Both of these RNAs are finally transferred from the nucleolus to the cytoplasm through the nuclear membrane. Different authors have given stress to the point that the role of the nuclear membrane is a gene-controlled reaction. Through the idea of the formation of RNA from DNA, the relationship between DNA and protein synthesis has been established.

It has also been found that the base ratio of DNA (*i. e.*, adenine-thymine : guanine-cytosine) holds an inverse relationship with the RNA of the same species. Though the way through which RNA is actually derived from DNA is not clearly known, still this inverse relationship suggests some correlation between these two nucleic acids.

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